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Biology and histopathology of Proteocephalus ambloplitis Liedy, 1887, infecting walleye (Stizostedion vitreum vitreum) and yellow perch (Perea flavescens) in Lake of the Woods, Ontario

Armstrong, Kimberly Blythe

THE BIOLOGY AND HISTOPATHOLOGY OF *Proteocephalus ambloplitis* LEIDY, 1887 (CESTODA: PROTEOCEPHALIDAE) INFECTING WALLEYE (*Stizostedion vitreum vitreum*) AND YELLOW PERCH (*Perca flavescens*) IN LAKE OF THE WOODS, ONTARIO

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ABSTRACT

Walleye (Stizostedion vitreum vitreum) and yellow perch (Perca flavescens) from Lake of the Woods were examined for parenteral Proteocephalus ambloplitis from May to November, 1982 and 1983. One hundred percent of the age 1 and older walleye and 74% of the age 1 and older yellow perch harboured plerocercoids. In corresponding age classes, walleye were generally 10 times more heavily infected than yellow perch. Mean intensity of live plerocercoids increased with age of walleye until age class 5 then declined significantly in older fish. Intensity increased from a mean of 23 (in age class 0) to a maximum of 171 in age class 5 and was only 58 in the 7+ age class. Mean intensity of plerocercoids increased continuously with the age of yellow perch from 2 (age class 0) to a maximum of 20 in the 5+ age class.

All age classes of walleye (0 to 7+) became infected by preying on yellow perch, particularly the young-of-the-year (YOY). Small yellow perch became infected by eating copepods but older perch obtained plerocercoids by cannibalism. The transmission of plerocercoids to walleye and yellow perch was greatest during late summer. Young-of-the-year walleye and YOY yellow perch first harboured plerocercoids in early August.

The liver was the first organ of walleye and yellow perch to be invaded by migrating plerocercoids. However, in

walleye, the mesenteries ultimately contained the greatest proportion of plerocercoids in age 1 and older fish. The liver remained a relatively important site for plerocercoids in all age classes of yellow perch. Relatively few plerocercoids were found in the gonads of walleye or yellow perch. Walleye fecundity was not correlated with plerocercoid intensity.

Ninespine sticklebacks (*Pungitius pungitius*) and logperch (*Percina caprodes*) were found to harbour *P. amblopliti*s plerocercoids. These are new host records.

Migrating plerocercoids caused the greatest pathological change in the liver of walleye and yellow perch. Zones of compressed and necrotic hepatocytes were evident adjacent to live, unencapsulated plerocercoids. The mesenteries of walleye were often fibrosed in response to large numbers of invading plerocercoids. The gastro-intestinal tract, posterior gonads and associated mesenteries were often compacted with fibrous tissue. Obstruction of the passage of gametes is possible. Constriction of the oviduct may result from the fibrous reaction. Also, encapsulated plerocercoids were found in the lumen of the oviduct creating a physical barrier. The wall of capsules encompassing plerocercoids in walleye was relatively thin (maximum of 90 microns) while in yellow perch, it was up to 290 microns thick.

ACKNOWLEDGEMENTS

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The time and effort volunteered by Jann Atkinson and Scott Lockhart during the field seasons 1982-83 is recognized and greatly appreciated. Without their help much of this work would not have been completed.

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INTRODUCTION

Smallmouth bass (_Micropterus dolomieui_), and presumably _Proteocephalus ambloplitis_ Leidy, 1887, were not known in Lake of the Woods prior to 1920. An initial survey of fishes from Lake of the Woods did not find smallmouth bass in these waters (Evermann and Latimer 1910). Smallmouth bass were first intoduced into Lake of the Woods during the early 1920's and they were probably infected with _P. ambloplitis_ . Since the initial introductions, the fish and parasite both, have flourished. In fact, many non-bass species in Lake of the Woods now harbour the larvae of _P. ambloplitis_ (Dechtiar 1972). The presence of _P. ambloplitis_ larvae in the body cavity of walleye (_Stizostedion vitreum vitreum_), the most economically important species in Lake of the Woods, has become a concern in recent years (V. Macins pers. comm.).

The accepted life history of _P. ambloplitis_ , which includes an obligate parenteral stage in the viscera of its definitive host, was determined by Fischer (1972). Eggs shed into the water column are consumed by copepods (Hunter 1928; Hunter and Hunter 1929; Fischer 1972). In the haemocoel of copepods the oncosphere develops to a plerocercoid I (terminology of Freeman 1964). Infected copepods are then eaten by many species of fish, including young bass, where the plerocercoid penetrates into the body cavity, is encapsulated and grows to a plerocercoid II. The life cycle is completed when a large bass consumes an infected small fish. If a large bass eats an infected small bass the plerocercoid II may mature directly in the intestine or it may enter the viscera of the large bass. But, if a large bass eats an infected non-bass fish then the plerocercoid II must enter the viscera of the definitive host. It can not mature directly in the intestine. Fischer and Freeman (1973) determined that *P. amblopli tis* plerocercoids have an obligate parenteral development in bass before they can mature.

The plerocercoids in the viscera of large bass are not at a dead end as was originally believed by Cooper (1915) and Hunter (1928). Parenteral plerocercoids can be stimulated to leave their parenteral sites and migrate back to the intestine. Fischer and Freeman (1969) determined that an increase in water temperature from 4 to $7^{o}C$ was the required stimulus in the laboratory as well as in smallmouth bass from Lake Opeongo. However, the migration of parenteral plerocercoids into the intestine was noted to occur only in mature bass suggesting the hormonal state of the host may enhance the effect of temperature (Fischer and Freeman 1969). Esch et al. (1975) also found that plerocercoid migration only occurred in mature bass from Michigan, however, the migration was stimulated at higher temperatures ($14^{o}C$ or greater) than reported by Fischer and Freeman (1969). Esch et al. (1975) then stressed the possibility that the migratory stimulus was hormonal, and not temperature dependent. At present, the controversy remains unresolved.

Apparently, *P. amblopliti*s can survive only where smallmouth and/or largemouth bass (*Micropterus salmoides*) reside (Fisher and Freeman 1973; Eure 1976; Freeman pers. comm.), Therefore, smallmouth and largemouth bass which are probably the only definitve hosts, will be referred to as 'natural' hosts. Other fish species in which there is no development further than the plerocercoid II stage and in which, the parasite is unlikely to be transferred to a suitable host are herein termed 'accidental' hosts. In this sense walleye and large yellow perch (*Perca flavescens*) are referred to as accidental hosts.

The terms plerocercoid I and plerocercoid II were proposed by Freeman (1964) to describe the life stages of *P. parallacticus* . Apparently, the plerocercoids in copepods and fish differed only in size with the plerocercoid II being 10 times as large as the plerocercoid I. Fischer and Freeman (1969) found the developmental stages of *P. ambloplitis* to be similar to *P. parallacticus* and proposed the same terminology for the former species. Throughout this study, 'plerocercoid' refers to the parenteral stage in fish, unless stated otherwise.

When plerocercoids invade the body cavity of fish pathological change may be incurred by the host, especially in heavy infections. Pathological damage to fish, particularly smallmouth bass, as a result of heavy plerocercoid infections has been well documented (Moore 1925; Bangham 1927a; Bangham 1927b; Langlois 1936; Esch and Huffines 1973; Hoffman 1975). It is not known if heavy plerocercoid infections will effect pathological change in accidental hosts, such as walleye and large yellow perch. The biology of P. amblopliitis has been studied intensively, however, the fate of plerocercoids infecting accidental hosts has not.

The present study was initiated to examine the biology and histopathology of P. amblopliitis plerocercoids in two percid accidental hosts, the walleye and yellow perch. The main objectives of this study were to:

1) determine the prevalence and intensity of plerocercoid infections in walleye and yellow perch with respect to age, size and sex;
2) determine which visceral areas harboured plerocercoids;
3) identify the source of plerocercoids infecting walleye and yellow perch;
4) describe the pathological changes associated with a plerocercoid infection in walleye and yellow perch and
5) assess the effect of a plerocercoid infection on walleye fecundity.

MATERIALS AND METHODS

Study area

Lake of the Woods ($49^{o}20'$ N; $94^{o}40'$ W) is located approximately 500 km west of Thunder Bay, Ontario. The lake has a total area of 387,151 ha, of which 64% (246,718 ha) is in Ontario (Ontario Ministry of Natural Resources, Kenora; unpubl.), 33% in Minnesota, U.S.A. (Carlander 1949), and the remainder in Manitoba, Canada. The portion in Ontario has a mean and maximum depth of 7.9 m and 68.8 m respectively. Lake of the Woods is part of the Hudson Bay drainage area (Carlander 1949) with Rainy River as its major tributary and the Winnipeg River the outlet.

This study was restricted to the southwest section of the lake within Ontario. This portion of the lake is bordered by French Portage Narrows, the International border, Rainy River and Sabaskong Bay to the north, west, south and east, respectively (Fig. 1).

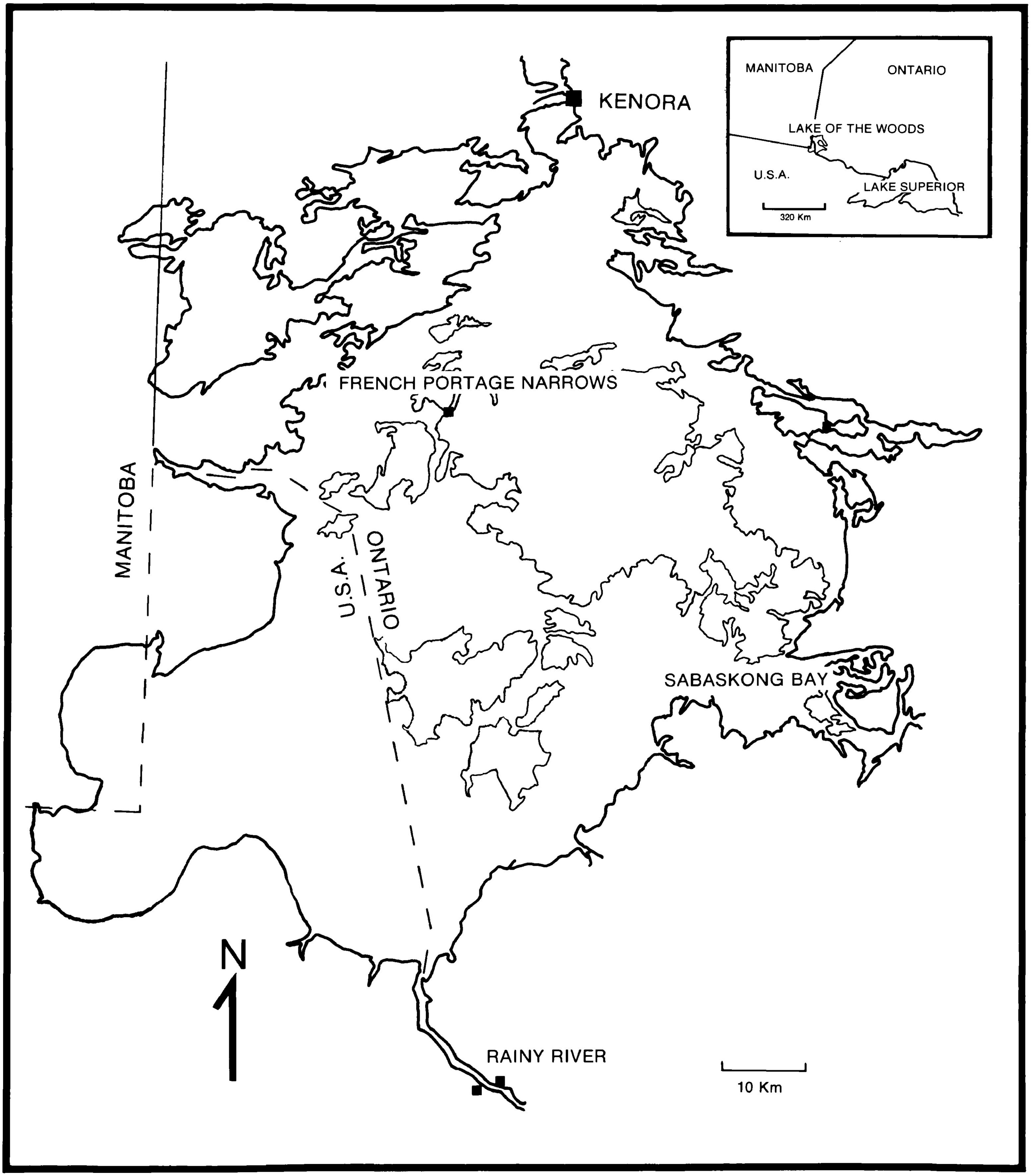
Examination of fish for parenteral P. amploplitis

Age one and older walleye and yellow perch

Age 1 and older walleye and yellow perch were sampled monthly from May to September 1983 and examined for *P. ambloplitis* plerocercoids. Walleye data were supplemented with preliminary collections made from June to August and November 1982.

Walleye and yellow perch were collected using gill nets

Fig. 1. Map of Lake of the Woods showing the borders of the study area. Inset shows geographical location of Lake of the Woods.


KENORA
MANITOBA
ONTARIO
LAKE OF THE WOODS
U.S.A.
LAKE SUPERIOR
320 Km
FRENCH PORTAGE NARROWS
MANITOBA
U.S.A.
ONTARIO
SABASKONG BAY
N
RAINY RIVER
10 Km

(1.9 to 12.7 cm, in 1.3 cm increments, stretched mesh) set overnight. Total length (nearest 1 mm), weight (nearest 10 g if greater than 100 g and nearest 1 g if less than 100 g) and sex were recorded for each fish. The left opercular bone, second dorsal spine and scales were removed for age determination.

Walleye and yellow perch were selected according to predetermined length classes to ensure equal sampling over most of the available size range. Walleye were separated into 7 length classes from 10 to 40+ cm in 5 cm increments. Yellow perch were separated into 6 length classes from 5 to 20+ cm in 3 cm increments. Thirty-five walleye and 30 yellow perch (5 from each length class) were sampled each month. Walleye age classes 7 and older and yellow perch age classes 5 and older were grouped for statistical analyses. The grouped walleye and yellow perch age classes are referred to as 7+ and 5+, respectively.

Fish were examined by carefully removing the lateral musculature to expose the intact viscera. The viscera were washed with fresh water to collect plerocercoids free in the peritoneal cavity. The wash was poured into a Baermann funnel and left to settle for a minimum of three hours. Contents were drained from the bottom and examined for *P. ambloplitis* plerocercoids.

The gastro-intestinal tract was severed at the esophagus and rectum and the viscera were removed from the peritoneal cavity. The gonads, spleen, gallbladder, liver and kidney were removed and examined individually. Each organ was pressed between two glass plates and scanned for plerocercoids using a Bausch & Lomb dissecting microscope at 20-30X. If the organ was large, it was sectioned into manageable pieces prior to pressing.

Stomach contents were removed (see feeding analyses) and the gastro-intestinal tract and mesenteries placed in a plastic bag with approximately 250 mL of pepsin digest solution (Meyer and Olsen 1971). When the mesenteries were digested the solution was poured into a Baermann funnel, diluted with fresh water and left to settle for a minimum of three hours. Contents were drained from the bottom and examined for P. ambloplitis plerocercoids. The entire viscera of small fish, less than 15 cm, were pressed between glass plates instead of being digested.

Proteocephalus ambloplitis was recognized by the presence of four distinct suckers, a prominent end organ, many calcium corpuscles and no acetabular glands (Befus and Freeman 1973; R. Freeman pers. comm.). These criteria apply only to live plerocercoids.

Preliminary analyses of walleye in 1982 indicated that although some infections appeared severe with large numbers of cysts visible in the viscera, few plerocercoids were obtained on digestion of the tissues. In these fish, many plerocercoids may have been dead. Only live plerocercoids were recovered using the digest technique. For this reason, walleye sampled in 1983 were assigned an index relative intensity upon visual examination. This assessment was based on the apparent number of live and dead plerocercoids visible in the viscera and peritoneal cavity. Each fish was assigned an intensity index of light (number of cysts visible estimated to be from 1 to 50), medium (51 to 200) or heavy (201+). The number of live plerocercoids from indexed fish was later determined by pressing and digesting the tissues. Also, in this manner, an index of intensity was recorded for 280 walleye sampled during July and August, 1982 to determine if apparent plerocercoid intensity was related to the size of fish.

Statistical analyses followed Daniel (1978) and Sokal and Rohlf (1981). The criterion for significance of all analyses was at the 95% level. Differences between sexes were tested with a Mann-Whitney U analysis. Age and season variations in plerocercoid intensity were examined using the Kruskal-Wallis ANOVA with multiple comparisons analysis. Tests of association were accomplished using Kendall's Tau rank correlation unless otherwise specified. Statistics were performed with the aid of a Vax 11/780 mainframe computer using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975).

Young-of-the-year walleye and yellow perch

Young-of-the-year (YOY) walleye and yellow perch were captured from June to September, 1983 using a 30 m bag seine and a small (1.9 cm stretched mesh) monofilament gill net.

YOY walleye data were supplemented with preliminary collections made during July and August, 1982. YOY walleye were differentiated from YOY sauger (*S. canadense*) according to the criteria of Nelson (1968). Total length (nearest 1 mm) was recorded for each fish, the peritoneal cavity opened and the viscera extracted.

The organs were separated from the mesenteries where possible and examined for parenteral plerocercoids by pressing each viscus between two glass plates or two microscope slides. The viscera of YOY yellow perch less than 40 mm long were examined with the aid of a Leitz/Wetzlar compound microscope at 100X. The viscera of YOY fish greater than 40 mm were examined using a Bausch & Lomb dissecting microscope at 20-30X.

Forage fish

Fishes considered to be potential prey items of walleye and yellow perch were examined for parenteral *P. ambloplitis* by inspecting the peritoneal cavity and pressing the viscera between glass plates. Fish were collected using seine, trawl or gill nets during July and August, 1982 and 1983 and identified to species according to Scott and Crossman (1973).

All fish examined during this study were identified according to Scott and Crossman (1973) but scientific and common names used herein follow Robins et al. (1980).

Feeding analyses

The stomach contents of walleye and yellow perch were collected and preserved in 10% formalin. The buccal cavity was examined for regurgitated food items and the intestine flushed with water with the aid of a 50 mL syringe and a 5 mm diameter plastic tube. All items recovered were included as stomach contents. Invertebrate food items were identified according to Pennak (1978) and Merritt and Cummins (1978). Amphipods were identified to genus where possible; all other invertebrates were classified to order. Fish prey items were identified to species, where possible, according to Scott and Crossman (1973). Body shape, colouration, bone structure, number of pyloric caecae and scales were criteria used to identify partially digested fish.

Volume (nearest 0.1 mL) and number of each prey item were determined for each stomach sample. Individual samples were combined to obtain a monthly total. The relative importance of each prey item was determined by comparing percentage frequency of occurrence and percentage total volume. Only the frequency of occurrence of each prey item was calculated for YOY walleye and YOY yellow perch.

Enteral cestodes

Walleye, yellow perch, smallmouth bass, black crappies (*Pomoxis nigromaculatus*), rock bass (*Ambloplites rupestris*) and pumpkinseeds (*Lepomis gibbosus*) were collected by gillnetting, trapnetting and angling from May to September, 1982 and 1983 and examined for adult *P. ambloplitis*. As it had been noted previously that some enteral cestodes of walleye were evacuated after the death of the host, only those fish that were alive when removed from the nets were examined for enteral *P. amblopltis*. Fish were sacrificed by cervical dislocation and the peritoneal cavity opened. The esophagus and rectum were severed and the gastro-intestinal tract removed. The stomach was opened and the gastro-intestinal tract placed in a plastic bag with fresh water for a minimum of two hours which facilitated the release of cestodes. When removed from the plastic bag, more water was flushed through the intestine with the use of a 50 mL syringe and a 5 mm plastic tube to dislodge any cestodes still attached. After a number of such washings, the intestine and pyloric caecae were opened and examined visually for any remaining tapeworms.

All tapeworms were saved and placed in a 12 cm diameter Petri plate with fresh water. To enhance the relaxation of the strobilae, the tapeworms were refrigerated in a fresh-water bath for a minimum of 12 hours. When the strobilae were relaxed, the scolex of each tapeworm was examined using a Bausch & Lomb dissecting microscope at 20-30X. The number of individuals of each genus was recorded. Representative specimens were preserved in hot 10% AFA. Cestodes greater than 10 cm in length were stretched on dry paper towelling and the fixative poured over them. Smaller tapeworms were placed directly in the fixative (R.

Appy pers. comm.). For long term storage of the cestodes the 10% AFA was replaced with 70% EtOH. All cestodes were stained with Semichon's aceto-carmine (Meyer and Olsen 1971), cleared in Oil of Cedarwood and mounted in Permount.

Fecundity

Twenty mature female walleye were collected in early November, 1982 for fecundity analyses. Fish were obtained from commercial fishermen at Windy Point (on Lake of the Woods), Ontario. The ovaries were separated from the remaining viscera, patted dry, weighed to the nearest 0.0001 g with a Sauter balance and preserved in 10% buffered formalin. The remaining viscera were examined for parenteral *P. ambloplitis* in the manner previously described for age 1 and older walleye and yellow perch. The 20 walleye examined here comprise the total number of fish sampled for plerocercoids during this month and alone, represent the November sample.

Fecundity was estimated by the gravimetric method (Bagenal and Braum 1978; Serns 1982). Preserved ovaries were weighed to the nearest 0.0001 g with a Mettler AC 100 balance. The tunica albuginea was removed so that the weight of the eggs could be determined. A minimum 5% subsample of eggs was excised from the mid-section of the left ovary and counted. The total number of eggs was obtained by direct proportion.

Histopathology

Fifty walleye and 20 yellow perch were collected for histopathological examination from June to September, 1982 and 1983, from Lake of the Woods. Fish were collected by gill netting, trap netting and seining. Only the fish that were alive when removed from the nets were kept for this study. Fish were sacrificed by cervical dislocation and then the peritoneal cavity was opened. Selected sections of the liver, spleen, gonads, gastro-intestinal tract and mesenteries were excised and preserved in 10% phosphate buffered formalin. Tissues were embedded in paraffin, sectioned at 6 to 10 microns, stained in Lillie's A & B (Lillie 1954) or Gomori's triple stain (Humason 1979). Photomicrographs were produced using a Zeiss C 35 camera mounted on a Zeiss compound microscope.

RESULTS

Parenteral *P. amblopliti*s

Walleye - One hundred percent of the age 1 and older walleye sampled were infected with parenteral *P. amblopliti*s (Table 1). There was no difference in intensity of infection between sexes (U = 3915; 79,95 df.). However, male and female walleye did differ with respect to gonadal infections. Only 46.8% (37 of 79) of the males examined had plerocercoids in the testes with a mean of 3.3 per fish, whereas 84.2% (80 of 95) of the ovaries contained plerocercoids (mean = 7.5). However, gonadal infections constituted a relatively small proportion of the total number of plerocercoids recovered and therefore, males and females were combined for statistical analyses.

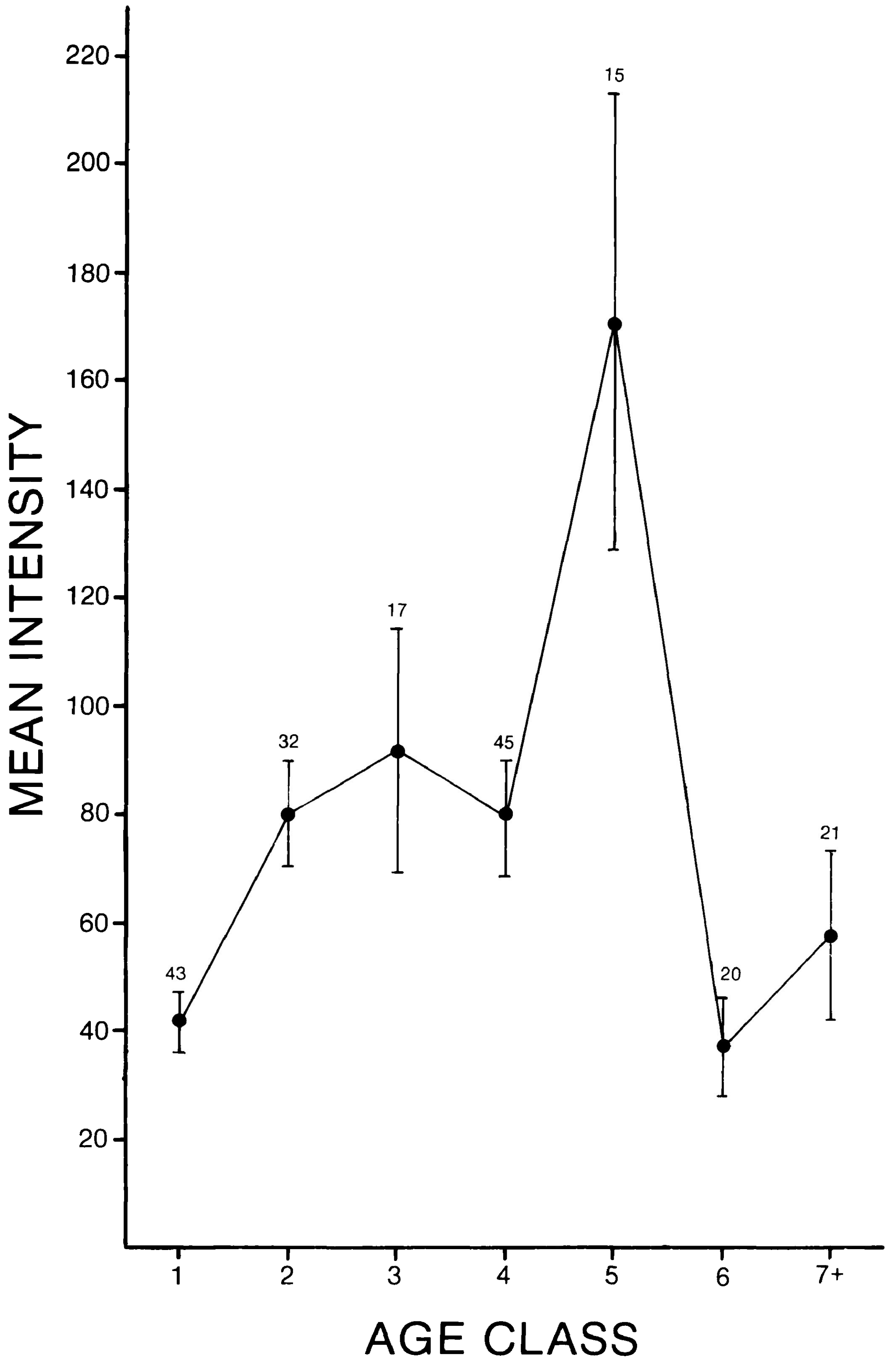
Mean intensity of parenteral *P. amblopliti*s in walleye increased significantly from 41.5 at age 1 to a maximum of 170.9 by age 5 (Table 1; Fig. 2). Mean intensity was significantly lower in older fish (36.8 and 57.6 in age classes 6 and 7+ respectively) (K-W ANOVA; X^2 = 28.8: 6 df.). The intensity of parenteral *P. amblopliti*s infection was positively correlated with length (Tau = 0.26), weight (Tau = 0.27) and age (Tau = 0.21) of walleye in age classes 1 to 5. Since length and weight were not correlated over the entire size range of walleye, further statistical analyses were performed only with respect to age. The mean number of parenteral *P. amblopliti*s

TABLE 1. Prevalence and mean intensity of parenteral P. *ambloplitis* plerocercoids in age one and older walleye from Lake of the Woods, Ontario, May to November, 1982 and 1983

Age class (yr)	Walleye examined: Number ♂♂	♀♀	Total	Total length (mm)	Weight (g)	Infected with P. *ambloplitis*: Prevalence %	Intensity
1	22	21	43	180 ± 5 †	52 ± 4	100	42 ± 6
				(120 - 244)	(10 - 110)		(1 - 152)
2	15	17	32	244 ± 7	133 ± 11	100	80 ± 10
				(178 - 310)	(47 - 240)		(8 - 270)
	7	10	17	302 ± 9	249 ± 21	100	92 ± 23
				(213 - 352)	(72 - 400)		(8 - 370)
4	24	21	45	347 ± 6	384 ± 20	100	79 ± 11
				(265 - 417)	(150 - 650)		(1 - 267)
5	4	11	15	397 ± 10	657 ± 42	100	171 ± 42
				(321 - 442)	(350 - 810)		(9 - 580)
6	4	16*	20	437 ± 6	811 ± 46	100	37 ± 9
				(390 - 500)	(450 - 1250)		(3 - 174)
7+**	3	18	21	460 ± 7	1012 ± 59	100	58 ± 16
				(399 - 504)	(580 - 1500)		(1 - 312)

* Excludes one walleye with 971 plerocercoids.
** Age class 7+ includes 13, 6, 1 and 1 fish, 7, 8, 9 and 10 yr old respectively.
† Values are means ± S.E. subtended by range.

Fig. 2. Mean intensity (+/- S.E.) of parenteral *P. ambloplitis* infecting age 1 and older walleye sampled May to November, 1982 and 1983. Sample sizes are indicated above each point.


MEAN INTENSITY
220
200
180
160
140
120
100
80
60
40
20
15
17
32
45
43
20
21
1
2
3
4
5
6
7+
AGE CLASS

recovered from all age classes of walleye remained relatively constant from May to November (mean = 60), except for the month of September (mean = 154) (Fig. 3).

The importance of some visceral organs as sites for harbouring parenteral P. amboplitis varied with age (Fig. 4). The mesenteries harboured the largest percentage (42.5%) of all parenteral P. amboplitis present in age 1 walleye. The proportion of plerocercoids recovered from the mesenteries increased to 80% by age 5 and remained at approximately 80% in age classes 6 and 7+. As walleye aged, the percentage of all parenteral plerocercoids found in the liver and free in the peritoneal cavity varied inversely with that found in the mesenteries. In YOY walleye, 47% of all parenteral P. amboplitis occurred in the liver. By age 3, and continuing to age 7+, less than 10% of the total infection was found in the liver. Similarly, 53% of all plerocercoid in YOY walleye were free in the peritoneal cavity during August, but one month later only 35% of all plerocercoids were free and by age 4 just 12% of all parenteral P. amboplitis were free. Approximately 10% of all plercercoids were free in the peritoneal cavity of walleye in age classes 5 to 7+.

The proportion of parenteral P. amboplitis infecting the gonads and spleen remained constant from September of the walleye's first year of life to age 7+ (Fig. 4). The gonads contained approximately 5% of the total plerocercoid burden and the spleen approximately 2.0%. The

Fig. 3. Mean intensity (+/- S.E.) of parenteral *P. amboplitis* infecting age 1 and older walleye in relation to month of sampling. Sample sizes are indicated above each point.

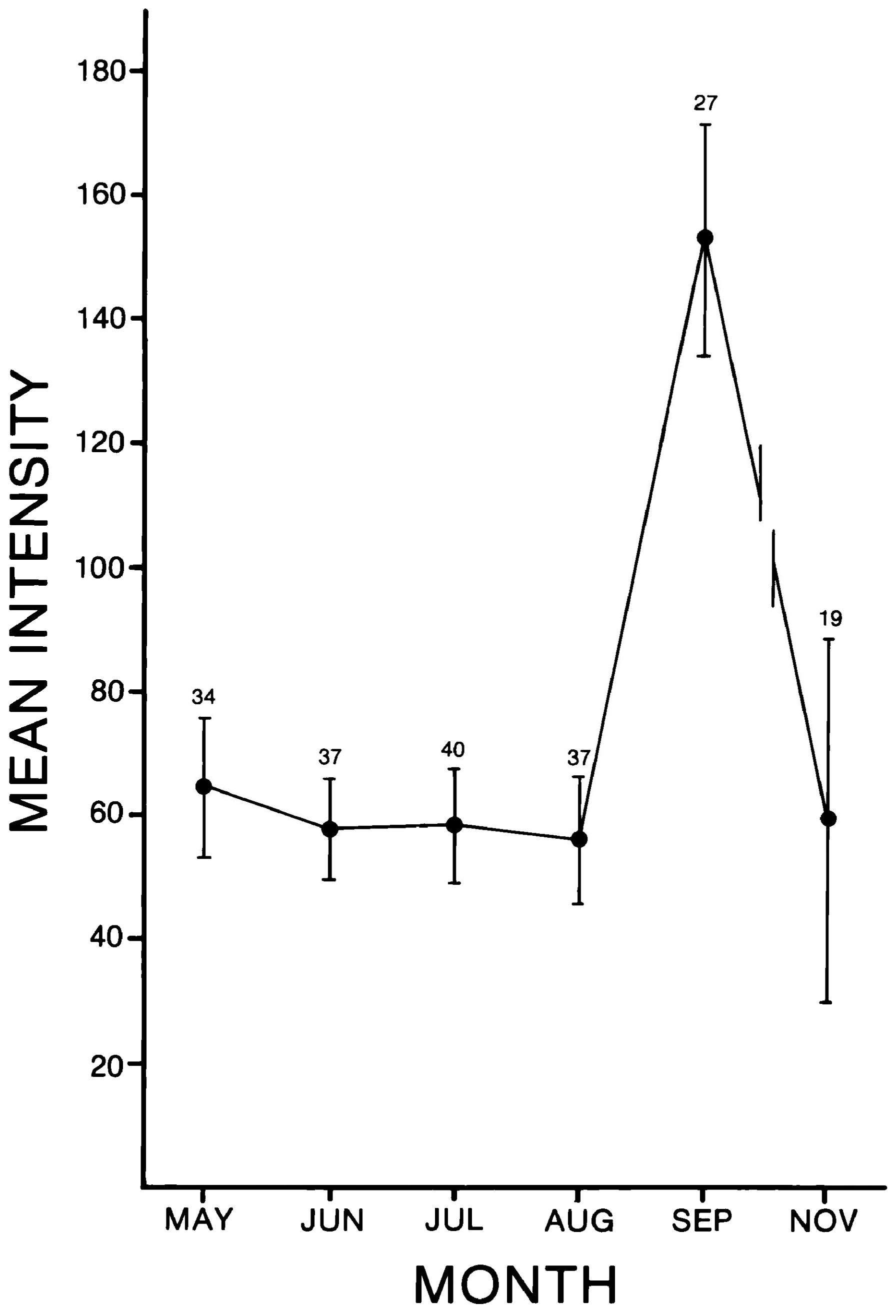
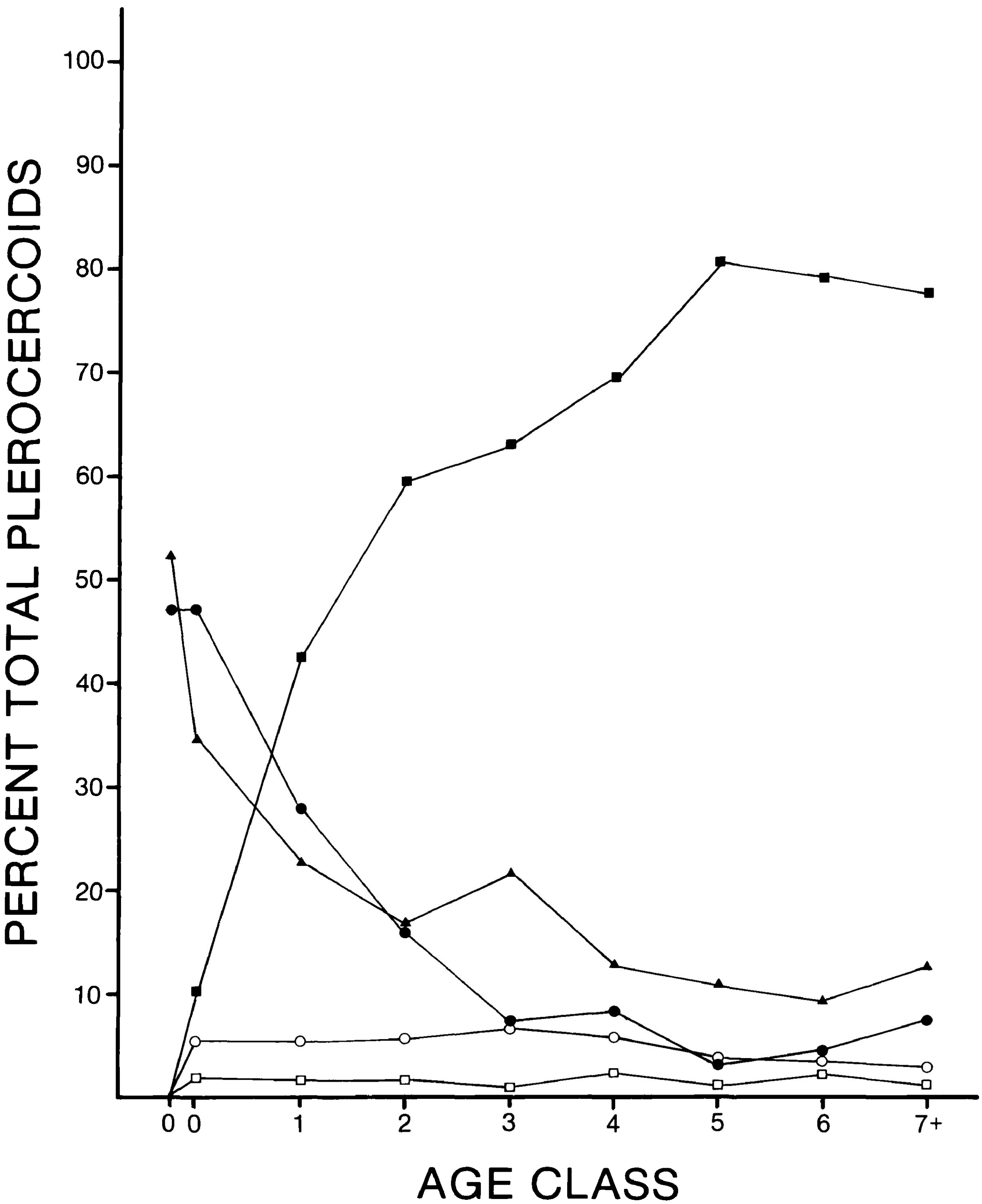

MEAN INTENSITY
180
160
140
120
100
80
60
40
20
34
37
40
37
27
19
MAY
JUN
JUL
AUG
SEP
NOV
MONTH

Fig. 4. Percent of total parenteral *P. amblop1itis* invading each visceral organ of walleye sampled May to November, 1982 and 1983. Young-of-the-year data is for August and September. Mesenteries (■); Free (▲); Liver (●); Gonads (○); Spleen (□).


PERCENT TOTAL PLEROCERCOIDS
100
90
80
70
60
50
40
30
20
10
0 0 1 2 3 4 5 6 7+
AGE CLASS

kidney and gallbladder of age one and older walleye each harboured less than 1% of the total parenteral P. ambloplitis infection.

Little monthly variation occurred with respect to the proportion of plerocercoids found in each visceral organ (Fig. 5). The percentage recovered from the mesenteries remained relatively constant at about 60% from May to September but increased to 89% by November. The percentage of all plerocercoids recovered from the liver declined from 19% in May to 5% by November. However, the November sample was comprised exclusively of age 5 to 7+ walleye that were obtained for the fecundity estimate. The percentages of total plerocercoids found in the gonads and spleen changed little from May to November. The percentage free in the peritoneal cavity increased from 5% in May to 18% by June and remained at approximately 18% until September. However, the percentage free in walleye was only 5% by November.

The mean number of parenteral P. ambloplitis recovered from some visceral organs varied with age (Table 2). The mean number of plerocercoids infecting the liver was significantly higher in age 1 and 2 walleye (11.6 and 12.7) than in fish older than age 5 (means less than 5) (X^2 = 55.5; 6 df.). The mean number of plerocercoids free in the viscera of walleye ages 1 to 5 was significantly greater than in age 6, but not age 7+ fish (X^2 = 25.2; 6 df.). The mean number of parenteral plerocercoids in the mesenteries demonstrated the greatest magnitude of change with age. The

Fig. 5. Percent of total parenteral *P. ambloplitis* invading each visceral organ of walleye in relation to month of sampling. Mesenteries (■); Free (▲); Liver (●); Gonads (○); Spleen (□).

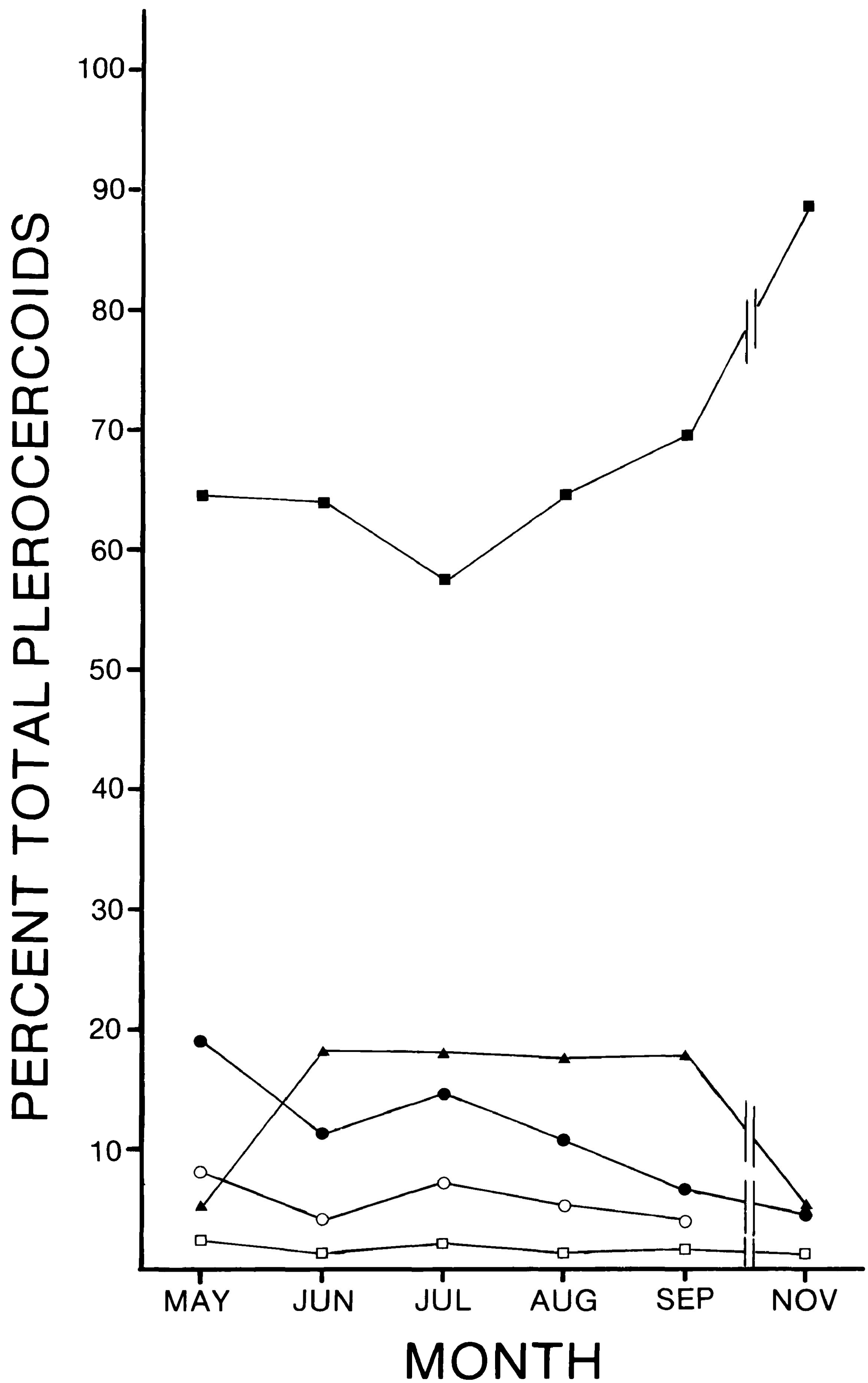

PERCENT TOTAL PLEROCERCOIDS
100
90
80
70
60
50
40
30
20
10
MAY
JUN
JUL
AUG
SEP
NOV
MONTH

TABLE 2. Mean number of parenteral *P. amblopli*tis plerocercoids in visceral organs of age one and older walleye sampled May to November, 1982 and 1983

Age class	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
1	43	2.2	0.7	0.1	11.6	0.1	9.2	17.6
2	32	4.5	1.4	0.2	12.7	0.2	13.2	47.8
3	17	6.4	0.9	0.1	6.5	0.1	20.0	57.8
4	45	4.4	1.9	0.4	6.7	0.2	10.2	55.3
5	15	6.7*	1.9	0.3	5.5	0.5	18.3	137.9
6	20	2.0**	0.8	0.3	1.7	0.1	3.5	29.2
7^+	21	3.2***	0.8	0	4.1	0	7.0	41.4

* N = 13.

** N = 13.

*** N = 11.

mean number found in the mesenteries more than doubled (17.6 to 47.8) from ages 1 to 2 and increased significantly to 137.9 by age 5. The mean numbers of plerocercoids found in the mesenteries of age 6 and 7+ walleye were significantly lower than age 5 fish (X^2 = 35.9; 6 df.). Mean numbers of plerocercoids recovered from the gonads, spleen, gallbladder and kidney were relatively low and demonstrated little change with age.

The mean number of plerocercoids free in the peritoneal cavity increased significantly from a low of 3.3 per fish in May to approximately 10 per fish during June, July and August with another significant increase to 26.8 per fish by September (X^2 = 55.7; 6 df.) (Table 3). The mean number of plerocercoids free in the peritoneal cavity was significantly lower in November (5.2 per fish) than in September. The mean number of plerocercoids recovered from the mesenteries was significantly greater in September than any other month (X^2 = 55.7; 6 df.). The mean number of parenteral plerocercoids in other visceral organs remained relatively constant from May to November. Although there was a decline in the mean number of plerocercoids found in the liver of walleye sampled in November it may not reflect a real change because the November sample consisted of older (age 5 - 7+) fish.

The percentage occurrence of parenteral *P. amblopiitis* in the visceral organs of walleye varied little with age (Table 4). The mesenteries were infected in no less

TABLE 3. Mean number of parenteral *P. amblopitis* plerocercoids in visceral organs of age one and older walleye in relation to month of sampling (1982 and 1983)

Month	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
May	34	5.3	1.5	0.4	12.4	<0.1	3.3	41.8
June	37	2.5	0.8	0.1	6.5	0.3	10.6	37.1
July	40	4.2	1.3	0.1	8.6	0.1	10.6	33.6
August	37	3.1	0.7	0.2	6.0	0.1	9.8	36.2
September	27	6.3	2.6	0.3	9.4	0.5	26.8	107.8
November	19		0.8	0.2	2.1	0.1	5.2	51.1

TABLE 4. Percent occurrence of parenteral *P. ambloplitis* plerocercoids in visceral organs of age one and older walleye sampled May to November, 1982 and 1983

Age class	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
1	43	42.3	30.2	7.0	97.7	11.6	97.7	81.4
2	32	84.4	65.6	15.6	96.9	12.5	93.8	96.9
3	17	82.4	47.1	5.9	94.1	5.9	88.2	94.1
4	45	64.4	60.0	26.7	86.7	17.8	77.9	95.6
5	15	92.3	60.0	26.7	86.7	33.3	100	100
6	20	64.3	50.0	20.0	65.0	5.0	75.0	100
7^+	21	54.5	38.1	0	57.1	0	85.7	95.2

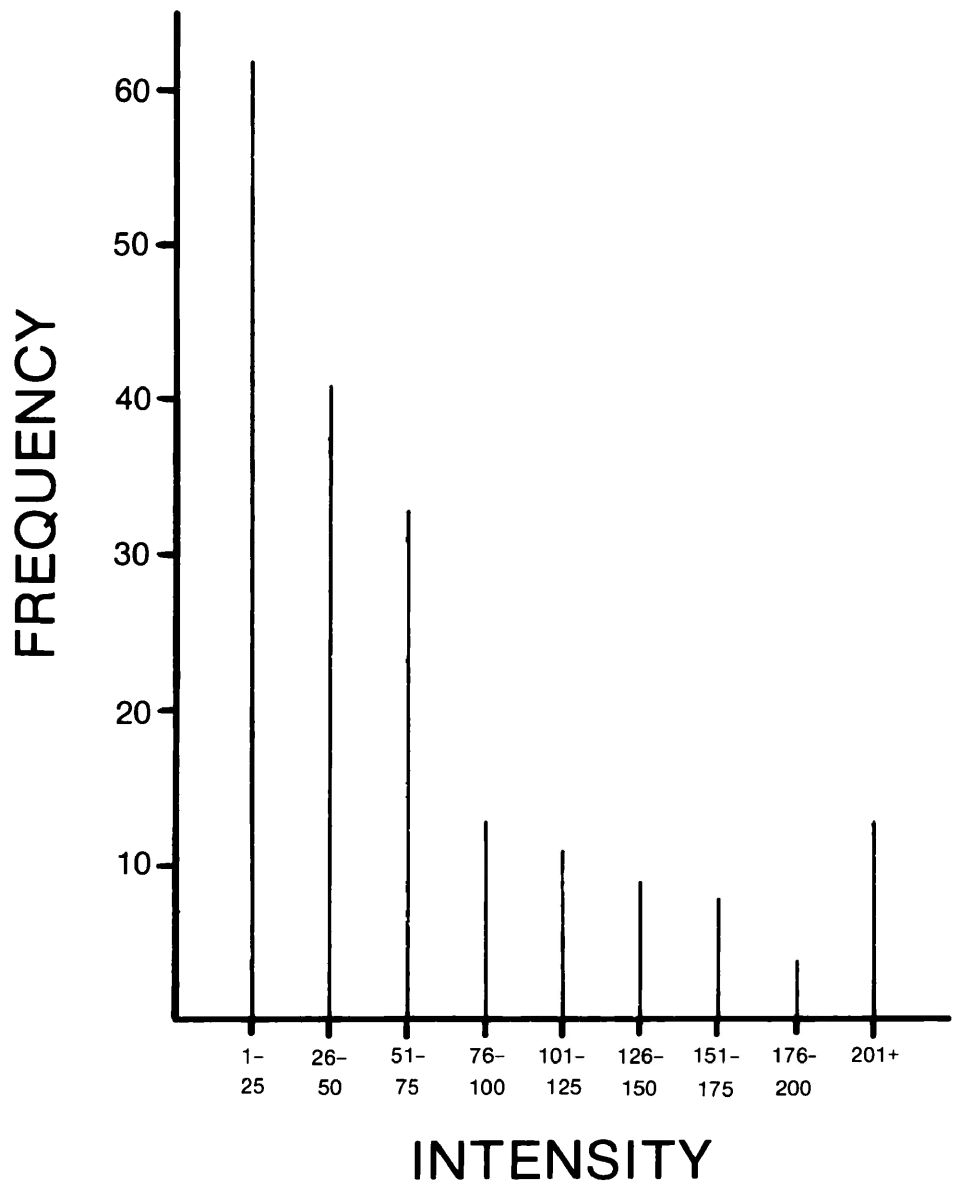
than 80% of the walleye sampled. Free plerocercoids were recovered from at least 75% of the walleye sampled from all age classes. The percent occurrence of plerocercoids found in the liver appeared to decrease, with increasing age of fish. Approximately 98% of the age 1 walleye had plerocercoids in the liver whereas only 57% of the age 7+ fish had a liver infection. The percent occurrence of plerocercoids in the gonads, spleen, gallbladder and kidney varied little with age. The monthly percentage occurrence of plerocercoids in the visceral organs examined was constant from May to November, except for September which consistently provided values greater than the other months (Table 5).

By the indexing method, it was apparent that some of the older and larger walleye in the population had infections that visually appeared heavy. Of the 193 walleye for which plerocercoid counts were done, 4 (2.1%) were judged to have heavy infections. These fish were a mean of 368 mm in length, weighed a mean of 465 g and were 4.3 years old. However, actual counts revealed that 13 (6.7%) had heavy infections of live plerocercoids, also 104 (53.9%) and 76 (39.4%) had light (1 - 50 plerocercoids) and medium (51 - 200) infections, respectively (Fig. 6). Thirteen (4.6%) of the additional 280 walleye indexed during 1982 were judged to harbour a heavy infection. These fish were a mean of 417 mm in length, weighed a mean of 911 g and were an average of 6.3 years old. While the indexing method underestimated the

TABLE 5. Percent occurrence of parenteral *P. amblopIitis* plerocercoids in visceral organs of age one and older *walleye* in relation to month of sampling (1982 and 1983)

Month	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
May	34	57.1	57.1	28.6	88.6	2.6	68.6	88.6
June	37	64.9	37.8	8.1	94.6	16.2	89.2	91.9
July	40	65.0	52.5	7.5	80.0	10.0	90.0	90.0
August	37	59.5	40.5	13.5	83.8	5.4	97.3	91.9
September	27	88.9	77.8	18.5	85.2	37.0	100	100
November	19		47.4	15.8	68.4	5.3	78.9	100

Fig. 6. Frequency of occurrence of parenteral *P. ambloplitis* intensities in age 1 and older walleye sampled May to November, 1982 and 1983.



FREQUENCY
60
50
40
30
20
10
1-
25
26-
50
51-
75
76-
100
101-
125
126-
150
151-
175
176-
200
201+
INTENSITY

number of walleye harbouring a heavy infection it did suggest that walleye appear to acquire plerocercoids continuously with increasing age. The distribution of parenteral P. ambloplitis in the walleye sampled did not fit a negative binomial distribution although the variance to mean ratio was much greater than 1 (6461/73 = 88.5). Such a large ratio indicates a very overdispersed population of live plerocercoids.

Yellow perch - Seventy-four percent (143/193) of the age 1 and older yellow perch sampled were infected with parenteral P. ambloplitis (Table 6). Prevalence increased from 59.4% at age 1 to almost 100% by age 5+. There was no difference in intensity between sexes (U = 2201; 54,89 df.). Only 8 of 54 (14.8%) infected male yellow perch had pleroceroicds in the testes with a mean of 2.9 per fish while 7 of 89 (7.9%) infected females had plerocercoids in the ovaries (mean = 1.3). Since plerocercoid infections in the gonads of male and female yellow perch were relatively rare and essentially the same, the sexes were combined for statistical analyses.

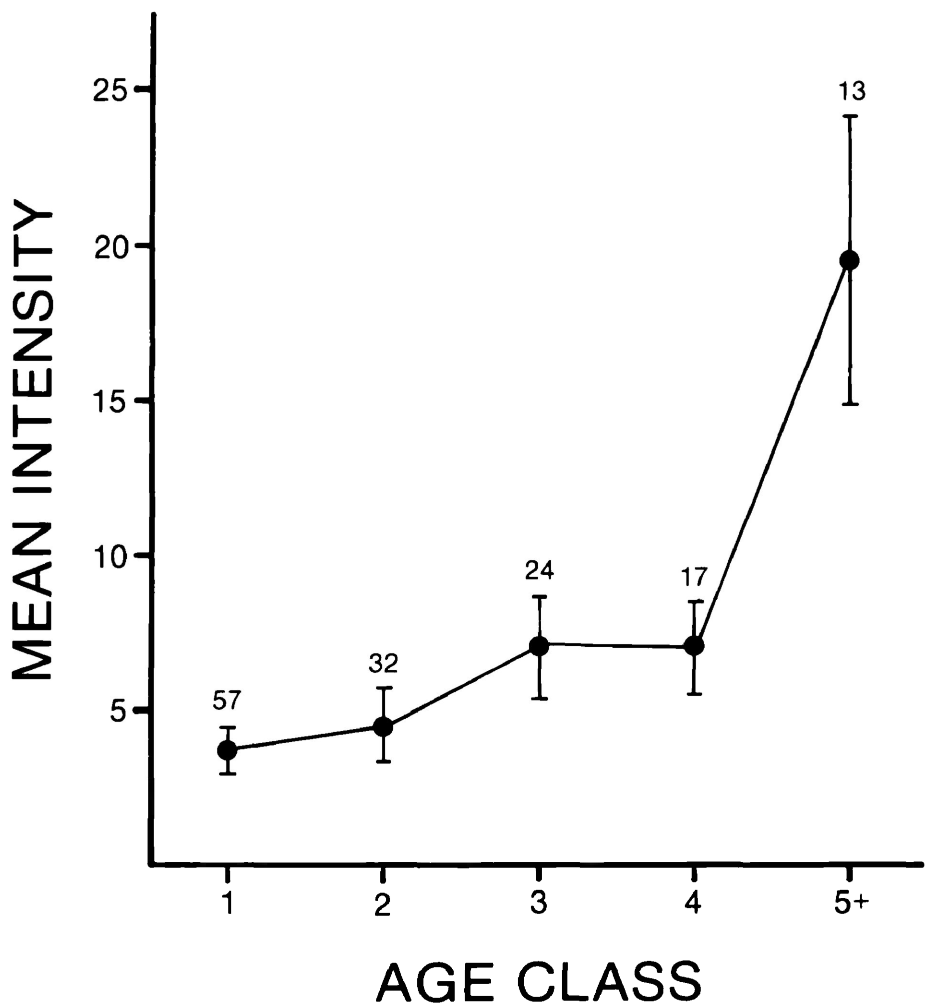
Mean intensity of parenteral P. ambloplitis increased significantly with age of yellow perch (K-W ANOVA; X^2 = 35.3: 4 df.) (Table 6; Fig. 7). Mean intensity increased from 3.2 at age 1 to 19.6 by age 5+. The intensity of parenteral P. ambloplitis infection was positively correlated with length (Tau = 0.37), weight (Tau = 0.29) and

TABLE 6. Prevalence and mean intensity of parenteral *P. amblopitis* plerocercoids in age one and older yellow perch from Lake of the Woods, Ontario, May to September, 1983

Age class (yr)	Yellow perch sampled: Number sampled ♂♂	♀♀	Total	Total length (mm)	Weight (g)	Number infected ♂♂	♀♀	Total	Prevalence %	Intensity
1	54	42	96	94 ± 3 †	14 ± 1	35	22	57	59.4	3 ± 1
				(49 - 140)	(3 - 32)					(1 - 37)
2	14	23	37	145 ± 3	42 ± 3	12	20	32	86.5	4 ± 1
				(99 - 195)	(11 - 95)					(1 - 39)
3	6	22	28	181 ± 4	81 ± 6	5	19	24	85.7	7 ± 2
				(152 - 231)	(40 - 130)					(1 - 32)
4	1	17	18	199 ± 5	95 ± 6	0	17	17	94.4	7 ± 2
				(173 - 260)	(60 - 130)					(2 - 28)
5^{+}*	2	12	14**	250 ± 9	206 ± 21	2	11	13	92.9	20 ± 5
				(189 - 305)	(83 - 360)					(2 - 49)

* Age class 5^{+} includes 5, 5, 1.2 and 1 fish 5, 6, 7, 8 and 10 yr old respectively.
† Values are means ± S.E. subtended by range.
** Excludes two fish, one with 73, the other with 293 plerocercoids.

Fig. 7. Mean intensity (+/- S.E.) of parenteral *P. amboplitis* infecting age 1 and older yellow perch sampled May to September, 1983. Sample sizes are indicated above each point.


MEAN INTENSITY
25
20
15
10
5
57
32
24
17
13
1
2
3
4
5+
AGE CLASS

age (Tau = 0.37) of yellow perch. To be consistent with the analyses for the walleye, all statistics were performed only with respect to age. The mean number of parenteral *P. amblopl*itis recovered from age 1 and older yellow perch varied only slightly with month of sampling (Fig. 8).

The proportion of all plerocercoids infecting the mesenteries and liver of yellow perch exhibited the greatest change with age (Fig. 9). Only 8% of all parenteral plerocercoids were found in the mesenteries of YOY yellow perch in September but increased to 48% by age 2. By age 5+, the mesenteries accounted for 69% of all plerocercoids found in the viscera of yellow perch. Conversely, the liver of YOY yellow perch harboured 66% of all plerocercoids by September but dropped to only 36% by age 2 and contained no more than 20% by age 5+. The percentage of all plerocercoids free in the viscera of yellow perch did not exhibit the same trend as in the walleye. Although the percentage free was greatest in younger fish it never exceeded 12% of total worm burden. The percentage of all plerocercoids recovered from the gonads and spleen remained relatively constant and low in all age classes of yellow perch. The gonads harboured from less than 1% to approximately 7.5% of all plerocercoids, and the spleen from 2% to 4.5%.

From all organs, the percentage of parenteral *P. ambloplitis* that were free in the viscera, in the mesenteries or in the liver varied the most from May to September (Fig. 10). The percentage of all plerocercoids

Fig. 8. Mean intensity (+/- S.E.) of parenteral *P. amploplitis* infecting age 1 and older yellow perch in relation to month of sampling. Sample sizes are indicated above each point.

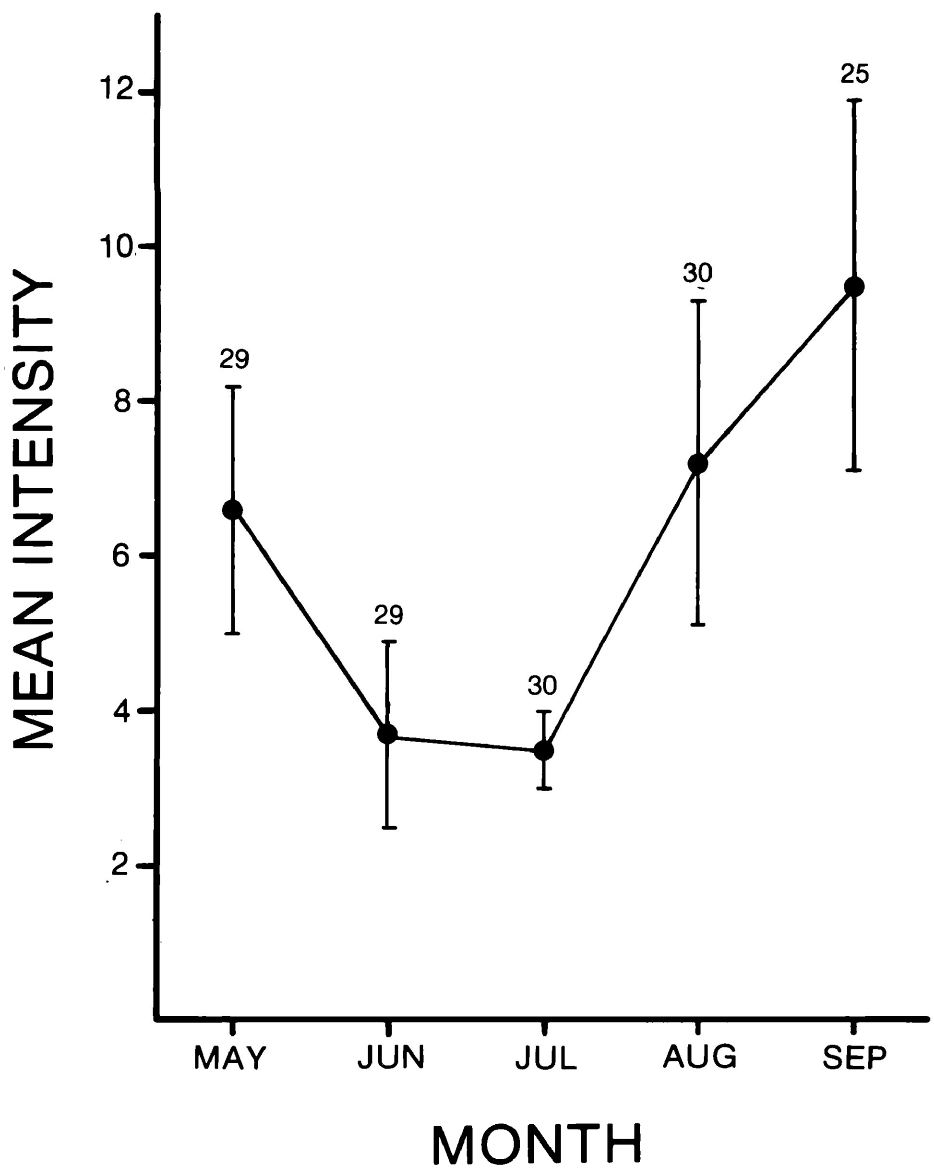
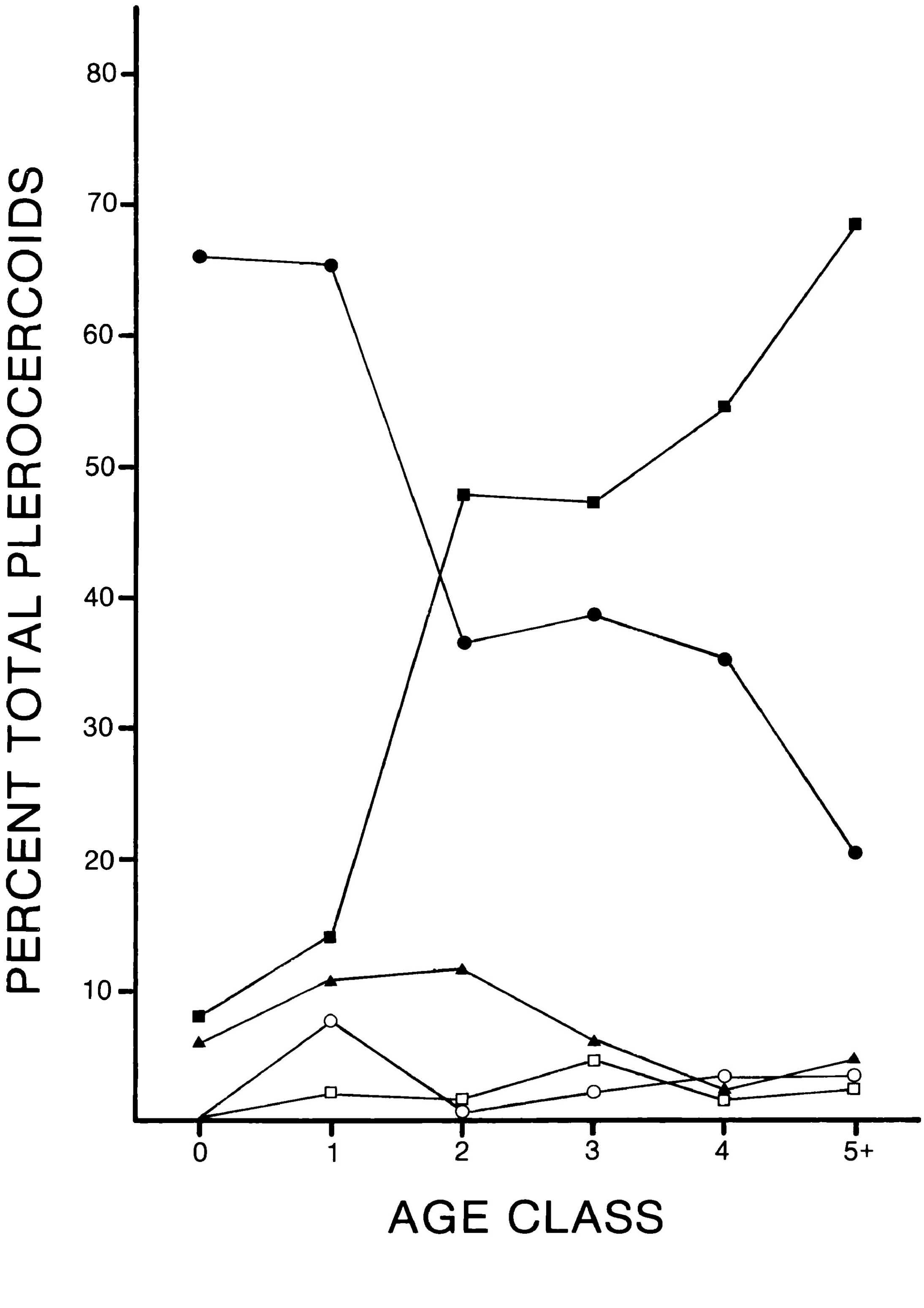
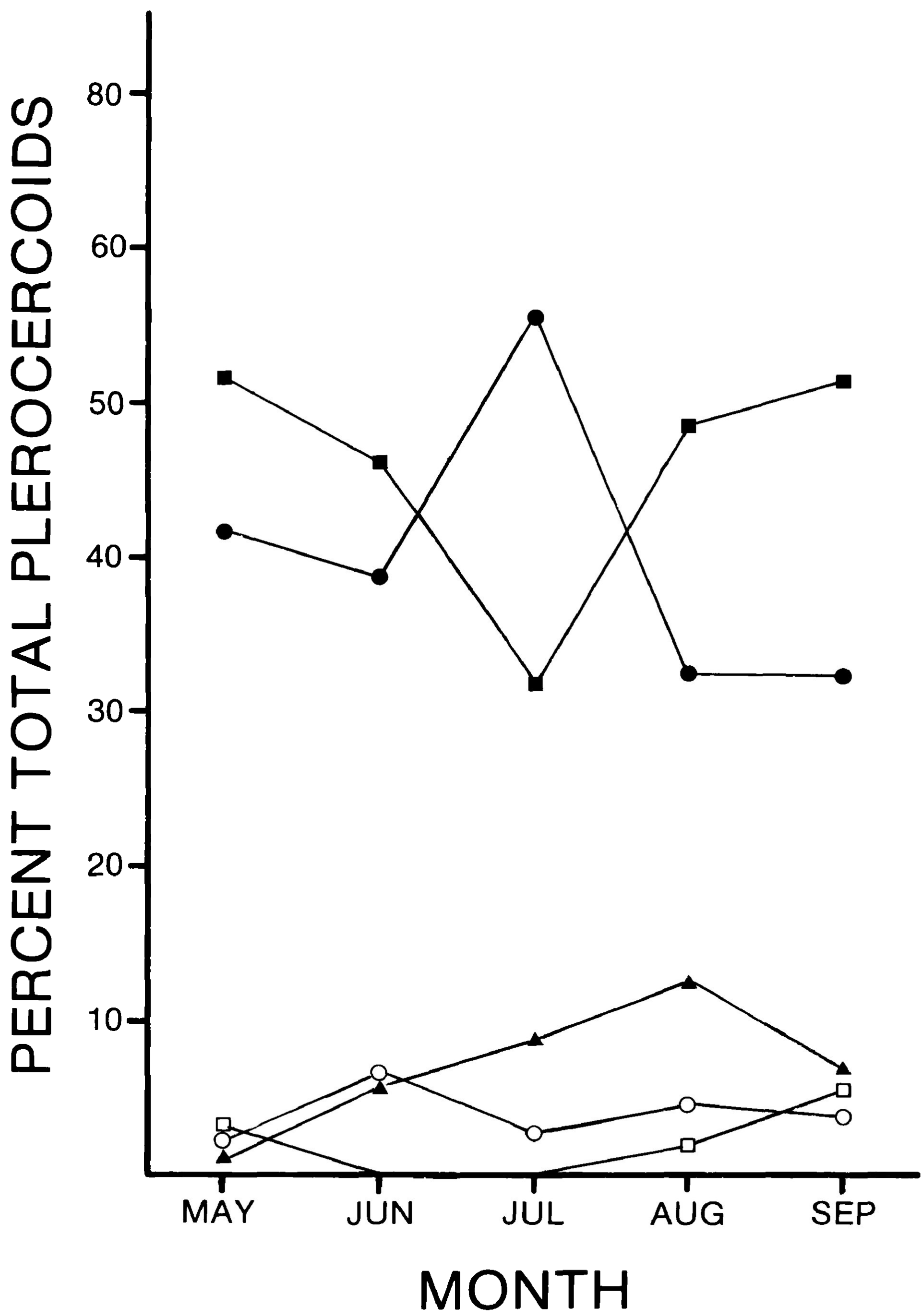

MEAN INTENSITY
12
10
8
6
4
2
29
29
30
30
25
MAY
JUN
JUL
AUG
SEP
MONTH

Fig. 9. Percent of total parenteral *P. amblopliti*s invading each visceral organ of yellow perch sampled May to September, 1983. Young-of-the-year data is for September. Mesenteries (■); Free (▲); Liver (●); Gonads (○); Spleen (□).



PERCENT TOTAL PLEROCERCOIDS
80
70
60
50
40
30
20
10
0
1
2
3
4
5+
AGE CLASS

Fig. 10. Percent of total parenteral _P. amboplitis_ invading each organ of yellow perch in relation to month of sampling. Mesenteries (■); Free (▲); Liver (●); Gonads (○); Spleen (□).



PERCENT TOTAL PLEROCERCOIDS
80
60
50
40
30
20
10
MAY
JUN
JUL
AUG
SEP
MONTH

recovered from the mesenteries varied inversely with the percentage of all plerocercoids recovered from the liver. The percentage recovered from the mesenteries declined from 52% in May to 32% by July but was again 52% during September. Conversely, the percentage recovered from the liver increased from 42% in May to 56% in July but then was lower (32%) in August and September. Unlike in walleye, the percentage of all plerocercoids that were free in the viscera of yellow perch increased gradually from 1% in May to a high of 12.5% by August. The percentage free was somewhat lower (7%) in September. The proportion of plerocercoids harboured in the spleen and the gonads was relatively constant throughout the sampling period.

The mean number of parenteral P. ambloplitis in the visceral organs of yellow perch did not increase greatly with age until the 5+ age class (Table 7). The mean number of plerocercoids in the gonads and spleen was less than 1 for all age classes. The gallbladder and kidney of yellow perch were rarely infected with plerocercoids. There was no significant difference in the mean number of free plerocercoids in the viscera, with increasing age of yellow perch (X^2 = 5.0; 4 df.). The mean number of plerocercoids in the liver of age 5+ fish was greater than that in age 2 fish. The mean number of plerocercoids found in the mesenteries increased significantly from 0.5 in age 1 fish to 13.5 in age 5+ fish (X^2 = 44.6; 4 df.).

There were no differences in the mean number of

TABLE 7. Mean number of parenteral *P. amblοplitis* plerocercoids in visceral organs of infected age one and older yellow perch sampled May to September, 1983

Age class	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
1	57	0.2	0.7	0	2.1	0	0.4	0.5
2	32	0.3	0.6	0.3	1.5	0.3	0.5	1.9
3	24	0.2	0.3	0	2.8	0	0.5	3.5
4	17	0.2	0.1	0.1	2.5	0.1	0.2	3.8
5^+	13	0.7	0.5	0	4.0	0	0.9	13.5

parenteral plerocercoids recovered between months from most visceral organs in all age classes of yellow perch (Table 8). There was a significant increase in the mean number of free plerocercoids in the viscera of yellow perch from May to August. The mean number of plerocercoids in the mesenteries did not vary over the summer (X^2 = 16.8; 4 df.)

The liver was the most frequently infected organ of age 1 and older yellow perch (Table 9). The liver was infected in 69% of the age 2, and 100% of the 5+ yellow perch. Although the mesenteries contributed the largest percentage to total infection in yellow perch age classes 2 to 5+, only 50% of the age 2 fish had plerocercoids in the mesenteries whereas by age 4, 88% of the fish were so infected. The frequency with which plerocercoids occurred in the spleen and gonads was similar. Even by age 2, yellow perch rarely harboured spleen or gonadal infections. The gonads were most frequently infected (20.8%) in age 3 fish, and the spleen (46.2%) in age 5+ yellow perch. The gallbladder and kidney were rarely parasitized by parenteral plerocercoids. The frequency of occurrence of plerocercoids free in the viscera was lowest (17.6%) in age 4 yellow perch and greatest (46.2%) in age 5+ fish.

The percentage occurrence of parenteral *P. ambloplitis* in each organ was relatively stable from May to September (Table 10). The liver was the most frequently infected organ in all months, followed by the mesenteries. The frequency of occurrence of free plerocercoids increased

TABLE 8. Mean number of parenteral *P. ambloplitis* plerocercoids in visceral organs of infected age one and older yellow perch in relation to month of sampling (1983)

Month	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
May	29	0.1	0.2	0	2.8	0	0.1	3.4
June	29	0.2	0	<0.1	1.4	0.1	0.2	1.7
July	30	0.1	0	<0.1	2.1	0	0.3	1.2
August	30	0.3	0.1	0	2.3	0	0.9	3.5
September	25	0.4	0.5	0	3.0	<0.1	0.6	4.9

TABLE 9. Percent occurrence of parenteral *P. ambloplitis* in visceral organs of infected age one and older yellow perch sampled May to September, 1983

Age class	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
1	57	8.8	3.5	0	93.0	0	21.1	15.8
2	32	3.1	3.1	3.1	68.8	3.1	18.6	50.0
3	24	20.8	20.8	0	75.0	0	37.5	66.7
4	17	11.8	11.8	5.9	76.5	5.9	17.6	88.2
5+	13	23.1	46.2	0	100	0	46.2	84.6

TABLE 10. Percent occurrence of parenteral *P. amblopl*itis plerocercoids in visceral organs of infected age one and older yellow perch in relation to month of sampling (1983)

Month	N	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
May	29	10.3	17.2	0	75.9	0	6.9	55.2
June	29	17.2	0	3.4	79.3	3.4	13.8	34.5
July	30	6.7	0	3.3	86.7	0	23.3	40.0
August	30	10.0	13.3	0	80.0	0	46.7	50.0
September	25	12.0	28.0	0	96.0	4.0	36.0	56.0

from 6.9% in May to 46.7% in August. A slight decline to 36.0% was apparent by September.

There were 10 or fewer parenteral plerocercoids in 89.5% (128 of 143) of the infected yellow perch (Fig. 11). Only 2 of 143 infected age 1 and older yellow perch harboured more than 50 plerocercoids. As in walleye, the distribution of parenteral *P. amblopIitis* in the yellow perch did not follow a negative binomial or a Poisson distribution. However, the population was determined to be over-dispersed as indicated by a variance to mean ratio of 13.5 (81/6).

Young-of-the-Year Walleye and Yellow Perch

Young-of-the-Year (YOY) walleye were first vulnerable to seining in July of both 1982 and 1983. However, YOY walleye were not infected with parenteral *P. ambloplitis* until August (Table 11). Prevalence and mean intensity were greater in August 1983 (93.2%; 5.6) than at the same time in 1982 (57.1%; 1.5). Virtually all (97.1%) of the YOY walleye sampled in September 1983 were infected with parenteral *P. ambloplitis* . The YOY walleye sampled in 1983 were generally larger than those sampled in 1982.

The majority of plerocercoids in newly infected walleye were free in the viscera (52%) or in the liver (47.7%) (Table 12). Mean numbers of plerocercoids recovered from each organ increased from August to September (Table 13). However, mean numbers of plerocercoids recovered from the

Fig. 11. Frequency of occurrence of parenteral *P. amblopitis* intensities in age 1 and older yellow perch sampled May to September, 1983.

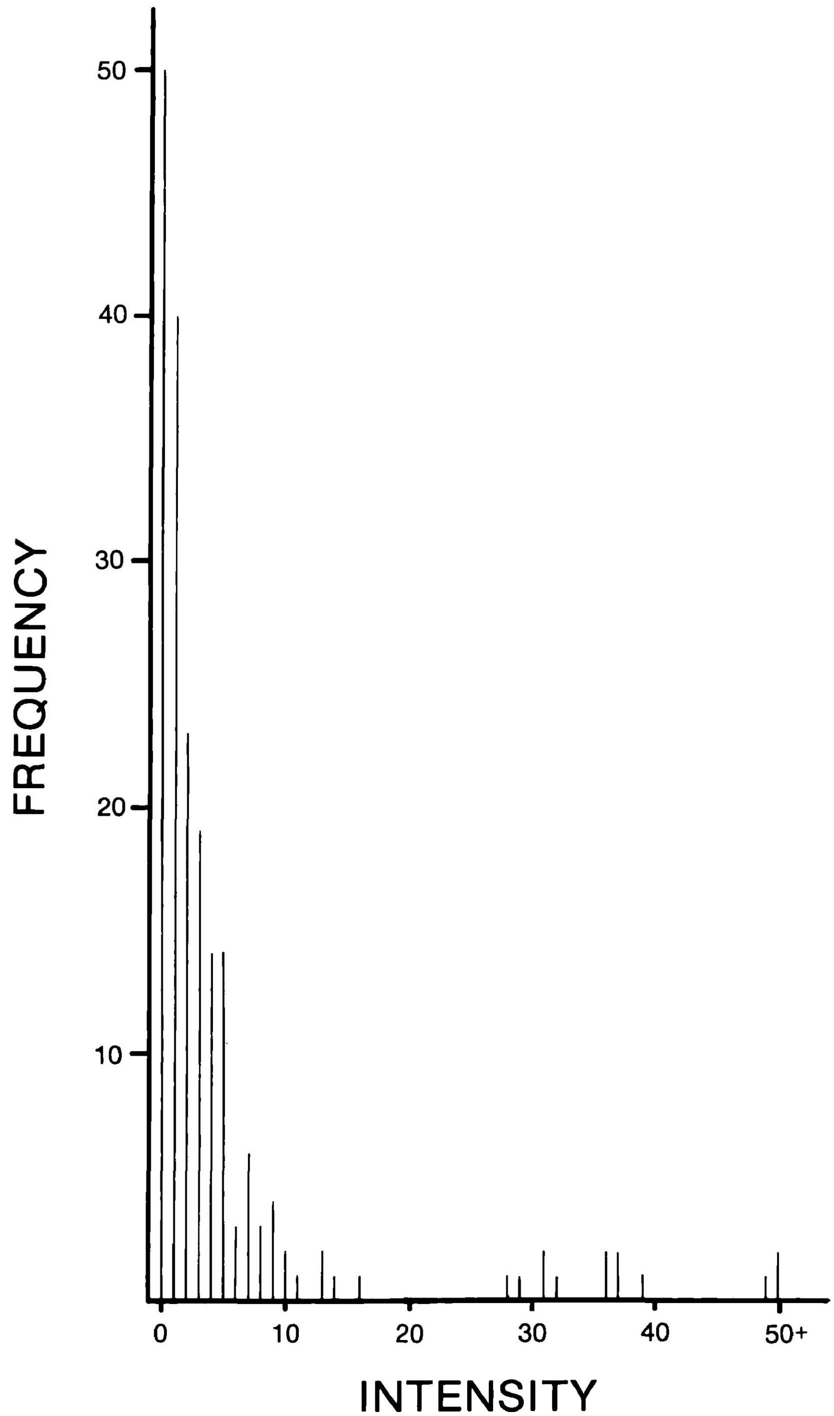

FREQUENCY
50
40
30
20
10
0
10
20
30
40
50+
INTENSITY

TABLE 11. Prevalence and intensity of parenteral *P. amblopIitis* plerocercoids in young-of-the-year walleye sampled July to September, 1982 and 1983, from Lake of the Woods, Ontario

			Fish total length(mm)		Prevalence	Intensity	
Year	Month	N	Mean	Range	(%)	Mean	Range
1982	July	52		43-76	0	0	0
	Aug.	14		60-95	57.1	1.5	1-3
1983	July	51	64.8	45-94	0	0	0
	Aug.	44	117.3	81-141	93.2	5.6	1-19
	Sept.	34	144.3	111-197	97.1	22.8	2-85

TABLE 12. Percent of total parenteral _P. amblopitis_ plerocercoids in visceral organs of infected young-of-the-year walleye sampled July to September, 1983

Month	No. infected	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
July	0/51	0	0	0	0	0	0	0
Aug.	41/44	0	0.4	0	47.4	0	52.2	0
Sept.	33/34	5.5	2.0	0	47.2	0.4	34.7	10.2

TABLE 13. Mean number of parenteral *P. amblоplitis* plerocercoids in visceral organs of infected young-of-the-year walleye sampled July to September, 1983

Month	No. infected	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
July	0/51	0	0	0	0	0	0	0
Aug.	41/44	0	<0.1	0	2.7	0	2.9	0
Sept.	33/34	1.2	0.5	0	10.8	0.1	7.9	2.3

visceral organs were still relatively low.

Pleroceroids free in the viscera occurred in almost 88% of the YOY walleye examined in August (Table 14). Liver infections were not as frequent at that time. However, by September 94% of the YOY walleye harboured a liver infection whereas 79% had pleroceroicds free in the viscera. Also, by September all the visceral organs, except the gallbladder, harboured at least one P. ambloplitis plerocercoid.

YOY yellow perch were first vulnerable to seining in June. YOY yellow perch did not harbour parenteral P. ambloplitis until August (Table 15). Prevalence of parenteral P. ambloplitis was 36.0% in August but doubled to 72.0% by September. However, mean intensity did not change from August to September.

The location of parenteral P. ambloplitis in the viscera of YOY yellow perch was recorded only in September. The liver harboured 82.1% (92 of 112) (mean intensity = 2.6) of all parenteral plerocercoids, 8.0% (9 of 112) (mean intensity = 0.3) were free in the peritoneal cavity and 9.8% (11 of 112) (mean intensity = 0.3) were already encapsulated. No plerocercoids were found in the other organs.

Unidentifiable plerocercoids were found in both YOY walleye and yellow perch during June and July 1983, but not later in the season. Two species or two developmental forms were seen. The first type which had four distinct suckers but no discernable end organ was found in 13.7% (mean

TABLE 14. Percent occurrence of parenteral *P. amblopliti*s plercercoids in organs of infected young-of-the-year walleye sampled July to September, 1983

Month	No. infected	Gonads	Spleen	Gallbladder	Liver	Kidney	Free	Mesenteries
July	0/51	0	0	0	0	0	0	0
Aug.	41/44	0	2.4	0	75.6	0	87.8	0
Sept.	33/34	30.3	30.3	0	93.9	9.1	78.8	12.1

TABLE 15. Prevalence and intensity of parenteral _P. amboplitis_ plerocercoids in young-of-the-year yellow perch sampled June to September, 1983, from Lake of the Woods, Ontario

		Fish total length(mm)		Prevalence	Intensity	
Month	N	Mean	Range	(%)	Mean	Range
June	50	23.2	16-27	0	0	0
July	50	34.4	30-48	0	0	0
Aug.	50	43.2	29-49	36.0	2.2	1-16
Sept.	50	58.0	45-70	72.0	2.9	1-8

intensity = 1.9) of the YOY walleye sampled in July. The same type was noted in 38.0% (1.5) of the YOY yellow perch sampled in June and 34.0% (1.6) in July. The second type which had an invaginated scolex and no discernable end organ or suckers was present in 26.0% (mean intensity = 2.2) of the YOY yellow perch sampled in July.

Forage Fish

The viscera of 731 potential forage fish, representing 22 species were examined for parenteral *P. amploplitis*. Only 9 species harboured *P. ambloplitis* plerocercoids (Table 16). YOY smallmouth bass (prevalence = 43.9%, 24 of 54), YOY sauger (42.9%, 6 of 14) and ninespine sticklebacks (27.9%, 17 of 61) were the most frequently infected species. The prevalence of plerocercoids was equal to or less than 10% in black crappies (2 of 20), YOY brown bullheads (1 of 10), YOY rock bass (4 of 71), brook sticklebacks (3 of 71) and log perch (*Percina caprodes*) (1 of 78). Mean intensities were low in all infected species. YOY smallmouth bass were the most heavily infected with a mean of 3.3 plerocercoids. Plerocercoids were not recovered from any species listed in Table 16 prior to August.

Adult cisco (*Coregonus artedii*) (N = 22), redhorse sucker (*Moxostoma* spp.) (1), quillback (*Carpoides cyprinus*) (1), white suckers (*Catastomus comersoni* (14) and sturgeon (*Acipenser fulvescens*) (3) were not infected with parenteral *P. ambloplitis*. Adult smallmouth bass (N

TABLE 16. Prevalence and intensity of parenteral *P. ambloplitis* recovered from forage fish sampled July to August, 1983, from Lake of the Woods

		N	Length(mm) Range	Prevalence(%)	Intensity Mean	Intensity Range
Smallmouth bass (YOY)*	*Micropterus dolomieui*	66	28 - 78	43.9	3.3	1-24
Sauger (YOY)	*Stizostedion canadense*	14	57 -127	42.9	1.5	1-3
Ninespine stickleback	*Pungitius pungitius*	61	24 - 40	27.9	1.4	1-2
Black crappie	*Pomoxis nigromaculatus*	20	39 - 55	10.0	1.5	1-2
Brown bullhead (YOY)	*Ictalurus nebulosus*	10	54 - 60	10.0	1.0	1
Rock bass (YOY)*	*Ambloplites rupestris*	111	15 - 37	4.5	1.4	1-3
Brook stickleback	*Culaea inconstans*	77	22 - 59	3.9	1.3	1-2
Logperch	*Percina caprodes*	78	30 - 81	1.3	1.0	1
Largemouth bass (YOY)	*Micropterus salmoides*	1	99	100.0	1.0	1
Troutperch	*Percopsis omiscomaycus*	37	25 - 92	0		
Burbot	*Lota lota*	3	33 - 43	0		
Sculpin	*Cottus* spp.	2	27 - 30	0		
Cisco (YOY)	*Coregonus artedii*	2	62 - 72	0		
Iowa darter	*Etheostoma exile*	4	45 - 58	0		
Johnny darter	*Etheostoma nigrum*	71	25 - 73	0		

TABLE 16 (continued)

		N	Length(mm) Range	Prevalence(%)	Intensity Mean	Intensity Range
Spottail shiner	Notropis hudsonius	36	23 -108	0	-	-
Emerald shiner	Notropis atherinoides	54	28 - 93	0		
White sucker (YOY)	Catastomus commersoni	48	41 - 79	0		
Blacknose shiner	Notropis heterolepis	21	25 - 63	0		
Golden shiner	Notemigonus crysoleucas	1	70	0		
Bluntnose minnow	Pimephales notatus	14	38 - 87	0		

* Combined data from 1982 and 1983.

= 13; prevalence = 100%), black crappies (30; 30%), pumpkinseeds (14; 7%), rock bass (6; 100%) and brown bullheads (11; 90%) were infected with plerocercoids.

Feeding analyses

Age 1 and older walleye preyed on both invertebrate and vertebrate food items throughout the sampling period (Tables 17 and 18). In May and June, larval insects were found in over 70% of walleye stomachs and accounted for approximately 60% of total food volume. Ephemeropteran nymphs were the most important larval insect eaten by walleye. Dipteran, coleopteran and plecopteran larvae were also recovered from walleye stomachs during the present study but were of minor importance.

Fish became increasingly important in the diet of walleye during the latter part of the summer. From July to September fish were present in over 70% of the walleye stomachs sampled. By September, 99.4% of total food volume consumed by walleye consisted of forage fish. Ninespine sticklebacks (*Pungitius pungitius*) and brown bullheads (*Ictalurus nebulosus*) were preyed upon early in the summer (May), but YOY yellow perch were the dominant forage fish from June to September. Twelve YOY yellow perch were eaten in June, 73 in July, 21 in August and 133 in September accounting for 30% to 86% of total food volume in walleye stomachs.

Age 1 and older yellow perch consumed a greater variety

TABLE 17. Percent occurrence of prey items in stomachs of age one and older walleye sampled May to September, 1983, from Lake of the Woods, Ontario

	Month				
	May	June	July	Aug.	Sept.
No. stomachs with food	23	22	24	21	26
Unidentifiable fish remains	8.7	9.1	41.7	47.6	26.9
Ninespine sticklebacks	21.7	13.6	0	0	7.7
Brown bullheads	4.4	0	4.2	0	0
Yellow perch	4.4	13.6	58.3	38.1	69.2
Spottail shiners	0	0	0	4.8	0
Sculpins	0	0	0	4.8	0
Total with fish	39.1	31.8	83.3	71.4	92.3
Unidentifiable insect remains	0	0	8.3	0	0
Ephemeropteran nymphs	69.6	63.6	50.0	28.6	7.7
Dipteran larvae	13.0	18.2	8.3	0	0
Coleopteran larvae	8.7	4.6	0	0	0
Plecopteran nymphs	0	4.6	0	0	0
Total with insects	79.3	72.7	58.3	28.6	7.7
Unidentifiable invertebrate remains	0	4.6	4.2	4.8	0
Leeches	8.7	4.6	8.3	9.5	0
Mysids	4.4	0	0	0	0
Amphipods	4.4	0	0	0	0
Snails	0	0	0	4.8	3.9
Plant material	0	0	0	0	3.9
Total other invertebrates	17.4	4.6	8.3	14.3	3.9

TABLE 18. Percent total volume of prey items in stomachs of age one and older walleye sampled May to September, 1983

	Month				
	May	June	July	Aug.	Sept.
No. stomachs with food	23	22	24	21	26
Total food volume (mL)	54.2	48.5	50.4	34.1	183.5
Unidentifiable fish remains	0.7	6.8	8.7	12.3	4.6
Ninespine sticklebacks	18.3	4.5	0	0	1.7
Brown bullheads	10.2	0	23.8	0	0
Yellow perch (≧ 1 yr)	5.5	0.6	14.9	42.8	6.8
(YOY)	0	30.9	26.2	21.4	86.4
Spottail shiners	0	0	0	13.2	0
Sculpins	0	0	0	0.9	0
Total with fish	34.7	42.8	73.6	90.6	99.4
Unidentifiable insect remains	0	0	2.2	0	0
Ephemeropteran nymphs	62.4	50.9	22.2	7.9	0.4
Dipteran larvae	0.2	0.4	0.4	0	0
Coleopteran larvae	0	5.6	0	0	0
Plecopteran nymphs	0	0.1	0	0	0
Total with insects	62.6	57.0	24.8	7.9	0.4
Unknown invertebrate remains	0	0.1	0.6	0.3	0
Leeches	1.7	0.2	1.2	0.6	0
Mysids	1.1	0	0	0	0
Amphipods	0.1	0	0	0	0
Snails	0	0	0	0.6	0.1
Plant material	0	0	0	0	0.1
Total other invertebrates	2.9	0.3	1.8	1.5	0.2

of food organisms than walleye (Tables 19 and 20). Larval insects occurred in at least 50% of the yellow perch stomachs from May to September but never accounted for more than 60% of total food volume. Total food volume was dominated by leeches in May and by amphipods in September. Yellow perch preyed less on fish than did walleye.

Ephemeropteran nymphs and dipteran larvae were consistently the most important insect prey items. No decline was evident in use of insects as prey items by yellow perch from May to September as was seen in walleye. Four other orders of insects were infrequently represented in the stomachs of yellow perch (Table 19).

Crustaceans were prey items for yellow perch throughout the study period, but were important only during August and September. Crayfish and amphipods were the two most important crustaceans in the diet of yellow perch. Amphipods alone accounted for 81% of total food volume in September. Other invertebrates, particularly leeches, were important early in the season (Table 20).

YOY walleye were piscivorous by July (Table 21). YOY yellow perch were the most important identifiable forage fish eaten by YOY walleye during the sampling period. Johnny darters (Etheostoma nigrum) and brook sticklebacks (Culaea inconstans) were of minor importance in the diet of YOY walleye. Invertebrates never occurred in more than 10% of the YOY walleye stomachs sampled.

YOY yellow perch preyed entirely on invertebrates

TABLE 19. Percent occurrence of prey items in stomachs of age one and older yellow perch sampled May to September, 1983, from Lake of the Woods, Ontario

	Month				
	May	June	July	Aug.	Sept.
No. stomachs with food	21	19	18	17	12
Unidentifiable fish remains	0	5.3	22.2	0	0
Johnny darters	4.8	0	5.6	5.9	0
Brook sticklebacks	0	0	5.6	0	0
Yellow perch	0	5.3	0	5.9	0
Total with fish	4.8	10.5	27.7	11.7	0
Unidentifiable insect remains	4.8	5.3	0	11.8	0
Ephemeropteran nymphs	23.8	73.7	50.3	41.2	41.7
Odonata larvae	14.3	5.3	5.6	0	0
Trichopteran larvae	14.3	10.5	0	5.9	0
Dipteran larvae	28.6	5.3	5.6	52.9	16.7
Lepidopteran larvae	4.8	0	0	0	0
Coleopteran larvae	4.8	10.5	0	0	8.3
Hemipteran larvae	0	5.3	5.6	0	0
Total with insects	71.4	78.9	61.1	88.2	50.0
Amphipods - *Hyalella*	14.3	0	0	0	25.0
- *Crangonyx*	4.8	0	0	0	100
- *Gammarus*	0	0	0	5.9	100
- unidentifiable	9.5	0	0	0	0

TABLE 19 (continued)

	Month				
	May	June	July	Aug.	Sept.
Cladocerans	0	5.3	0	0	16.7
Crayfish	0	0	16.7	11.8	0
Total with crustaceans	23.8	5.3	16.7	17.6	100
Unidentifiable invertebrate remains	0	15.6	16.6	0	0
Mysids	0	0	0	0	16.7
Leeches	14.3	5.3	0	0	0
Snails	9.5	0	0	0	0
Total other invertebrates	23.8	5.3	16.6	0	16.7

TABLE 20. Percent total volume of prey items in stomachs of age one and older yellow perch samples May to September, 1983

	Month				
	May	June	July	Aug.	Sept.
No. of stomachs with food	21	19	18	17	12
Total food volume (ml)	10	11.5	5.7	8.2	5.1
Unidentifiable fish remains	0	2.6	8.8	0	0
Johnny darters	3.0	0	0	1.1	0
Brook sticklebacks	0	0	29.8	0	0
Yellow perch (≥ 1 yr)	0	26.1	0	0	0
(YOY)	0	0	0	7.6	0
Total with fish	3.0	28.7	38.6	8.7	0
Unidentifiable insect remains	2.0	2.6	0	1.1	0
Ephemeropteran nymphs	17.1	47.0	33.3	39.1	14.9
Odonata larvae	11.1	0	0.9	0	0
Trichopteran larvae	3.0	2.6	0	1.1	0
Dipteran larvae	5.0	<0.1	<0.1	10.9	2.0
Lepidopteran larvae	<0.1	0	0	0	0
Coleopteran larvae	0	1.7	0	0	0
Hemipteran larvae	0	8.7	0	0	0
Total with insects	38.2	62.6	34.2	52.2	16.9
Amphipods - *Hyalella*	1.5	0	0	0	0
- *Crangonyx*	0.5	0	0	0	79.2
- *Gammarus*	0	0	0	0	0
- unidentifiable	0.5	0	0	0	0

TABLE 20 (continued)

	Month				
	May	June	July	Aug.	Sept.
Cladocerans	0	<0.1	0	0	2.0
Crayfish	0	0	4.4	39.1	0
Total with crustaceans	2.5	0	4.4	39.1	81.2
Unidentifiable invertebrate remains	0	7.8	22.8	0	0
Mysids	0	0	0	0	2.0
Leeches	44.2	0.9	0	0	0
Snails	12.1	0	0	0	0
Total other invertebrates	56.3	8.7	22.8	0	2.0

TABLE 21. Percent occurrence of prey items in stomachs of YOY walleye sampled July to September, 1982 and 1983, from Lake of the Woods, Ontario

	Month		
	July	Aug.	Sept.*
No. stomachs with food	55	38	20
Unidentifiable fish remains	80.0	36.8	65.0
Yellow perch (YOY)	14.5	60.5	20.0
Johnny darters	1.8	0	0
Brook sticklebacks	0	0	5.0
Total with fish	96.4	97.9	80.0
Unidentifiable invertebrate remains	5.5	5.3	0
Amphipods	0	0	5.0
Dipteran larvae	0	0	5.0
Total with invertebrates	5.5	5.3	10.0

* Data from 1983 only.

during the sampling period (Table 22). Crustaceans were found in over 80% of YOY yellow perch stomachs sampled June to September. Daphnia , species of copepods and amphipods occurred most frequently in the stomachs of YOY yellow perch. Copepods were found in the greatest numbers early in the season (May and June). Larval insects were rare in the diet of YOY yellow perch.

Enteral Cestodes

Bothriocephalus cuspidatus Cooper, 1917 was recovered from walleye, smallmouth bass and yellow perch, but occurred most often in walleye (prevalence = 80.3%; mean intensity = 24.3) (Table 23). Smallmouth bass were infected most often by P. ambloplitis (prevalence = 48.3; mean intensity = 5.1). One segmented, immature specimen of P. ambloplitis with developing genitalia was recovered from the intestine of a walleye.

All P. ambloplitis (4 of 4) recovered from smallmouth bass prior to mid June were immature. However, by late June almost half (16 of 34) of the specimens were gravid and by mid July, 12 of 13 idividuals recovered were gravid. During August, only half (7 of 14) of the P. ambloplitis recovered from smallmouth bass were gravid. All 5 individuals recovered from the intestine of smallmouth bass during September were immature.

Proteocephalus stizostethi Hunter and Bangham, 1933 and Triaenophorous nodulosus Pallas, 1760 were the two

TABLE 22. Percent occurrence of prey items in stomachs of YOY yellow perch sampled June to September, 1983, from Lake of the Woods, Ontario

	Month			
	June	July	Aug.	Sept.
No. stomachs with food	26	42	39	49
Unidentifiable insect remains	3.8	2.4	0	0
Dipteran larvae	0	7.1	5.1	22.5
Chironomids	0	4.8	0	0
Coleopteran larvae	0	0	2.6	0
Total with insects	3.8	11.9	7.7	22.5
Unidentifiable crustaceans	0	23.8	2.6	16.3
Daphnia	57.7	33.3	69.2	20.4
Cladocerans	7.7	0	0	0
Ostracods	0	7.1	0	0
Copepods	23.1	31.0	12.8	2.0
Amphipods	11.5	31.0	20.5	51.0
Total with crustaceans	92.3	90.5	92.3	81.6
Unidentifiable invertebrate remains	3.9	2.4	2.6	0

TABLE 23. Prevalence and intensity of enteral cestodes from three fish species sampled June to September, 1982 and 1983, from Lake of the Woods, Ontario

	Number			Prevalence	Intensity	
	Examined	Infected	Cestode spp.	(%)	Mean	Range
Walleye	61	58	*Bothriocephalus cuspidatus*	80.3	24.3	1-100
			Proteocephalus stizostethi	57.4	11.7	1-55
			Triaenophorous nodulosus	4.9	10.3	1-20
			Proteocephalus ambloplitis	1.6	1.0	1
Yellow perch	41		*Proteocephalus pearsei*	2.4	1.0	1
			Bothriocephalus cuspidatus	2.4	1.0	1
Smallmouth bass	29	15	*Proteocephalus ambloplitis*	48.3	5.1	1-14
			Proteocephalus spp.	17.2	1.8	1-14
			Bothriocephalus cuspidatus	3.4	2.0	2

other species of tapeworms recovered from the intestine of walleye. An unidentified species of *Proteocephalus* was found infecting smallmouth bass and the single infected yellow perch harboured another cestode, an individual *P. pearsei* La Rue, 1919.

Rock bass (N = 7), black crappies (5) and pumpkinseeds (2) were not infected with enteral cestodes.

Fecundity

There was no correlation between the intensity of plerocercoid infecton and fecundity of walleye (Pearson correlation coefficient; r = -0.07). The intensity of plerocercoids infecting these fish are reported as the November sample. Estimated fecundity of walleye aged 5 to 8 ranged from 32,625 to 102,457 eggs/female. Mean fecundity was 63,613 eggs/female (Table 24). Fecundity was linearly correlated with length, weight and age (Pearson correlation coefficient) (Table 25). The strongest correlation was with weight. The walleye ranged in size from 432 - 503 mm in total length (mean = 465) and 750 - 1,380 g in weight (mean = 1,001). Therefore, walleye produced a mean of 64 eggs per g of female.

Histopathology

Gross description

The term 'capsule' is used here in the sense of Sommerville (1981) and Rosen and Dick (1984).

TABLE 24. Mean fecundity (±S.E.) of walleye from Lake of the Woods, Ontario, 1982

Age class	N	Fecundity Mean	Fecundity Range
5	2	54649 ± 5435	49213 - 60084
6	8	56284 ± 1972	49429 - 61946
7	6	60674 ± 7190	32625 - 82516
8	4	87163 ± 5959	74041 - 102457
Total	20	63613 ± 3669	32625 - 102457

TABLE 25. Linear regression formulae for relationships between fecundity and length, weight and age of walleye from Lake of the Woods, Ontario, 1982

	r
Fecundity = 525 (Length) - 180732	0.64 *
Fecundity = 81 (Weight) - 17632	0.89 *
Fecundity = 11231 (Age) · 10514	0.64 *

*Significant at the 95% level.

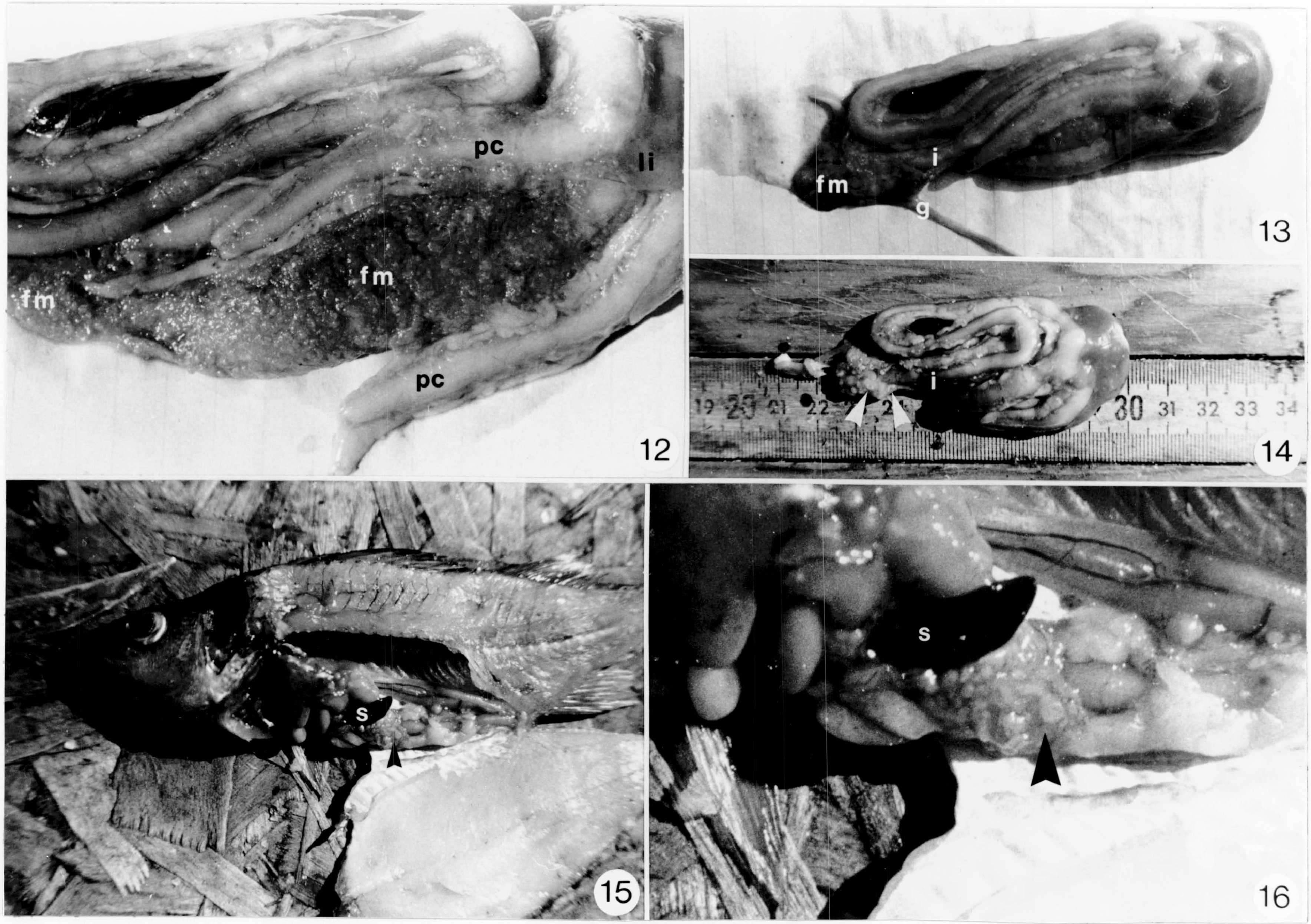
Heavy infections of P. ambloplitis plerocercoids in walleye caused severe visceral fibrosis and adhesions of the visceral mass to the peritoneum. The stomach wall was often fibrosed, being hard with small nodular capsules protruding from the tunica muscularis and serosa. Fibrosis and adhesions of the mesenteries and organs was most severe in two regions. The first encompassed the pyloric caeca, stomach, liver and associated mesenteries (Fig. 12). Adhesions of this mass to the anterior intestine were common. The second area was along the last 2 to 4 cm of the intestine (Fig. 13). The posterior gonads, ductus deferens or oviduct, and rectum were often aggregated in a fibrous mass.

Capsules surrounding plerocercoids in walleye varied in length from less than 1 mm to approximately 3 mm and were 'comma' shaped. The larger capsules were typically white and soft, and were associated with little or no visceral fibrosis (Fig. 14). The capsules associated with severe visceral fibrosis were small, yellow/brown in colour and hard. In yellow perch, capsules surrounding plerocercoids were discrete, with little or no associated fibrous reaction. Capsules were round, 1 to 3 mm in diammeter, white and hard (Figs. 15 and 16). Encapsulated plerocercoids appeared to be randomly located in the mesenteries of yellow perch.

Light microscopy

Liver - Wandering plerocercoids in the liver of walleye

Figs. 12 - 16. Fig. 12. Fibrosis of the stomach wall and connecting mesenteries (fm) with adhesions to the pyloric ceacae (pc) and liver (li) in an age 8 walleye. Fig. 13. Fibrosis of the mesenteries (fm) including the lower intestine (i) and posterior gonads (g) of an age 4 walleye. Fig. 14. A light plerocercoid infection showing the characteristic 'comma' shaped capsule (arrows) and little visceral fibrosis in an age 3 walleye. (i),intestine. Fig. 15. Encapsulated plerocercoids (arrows) in the fat of the mesenteries of an age 5 yellow perch. (s), spleen. Fig. 16. Enlarged view of the previous figure.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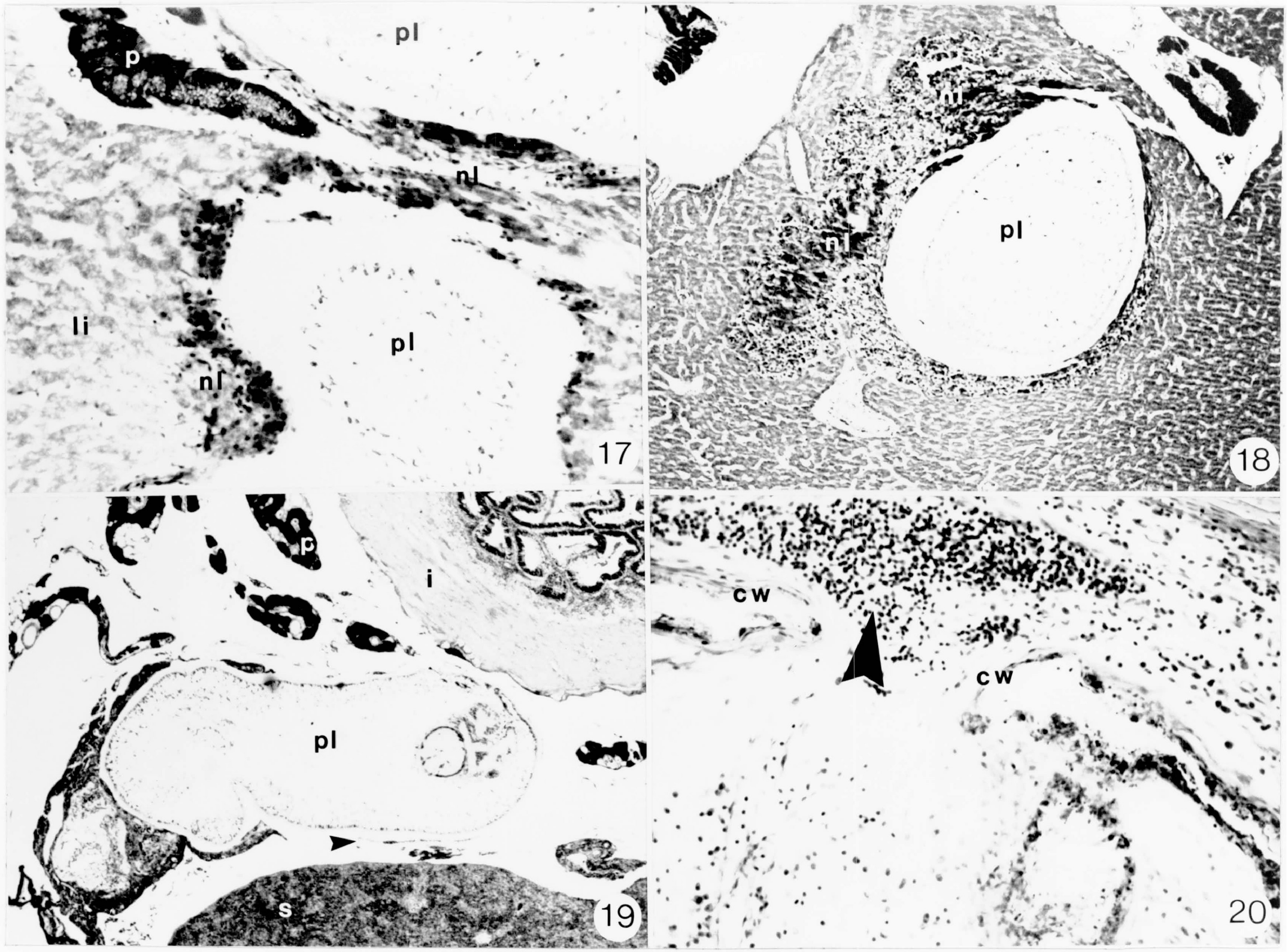
and yellow perch caused displacement and compression of hepatic cords. Migrating plerocercoids left well demarcated trails of necrotic hepatocytes and scar tissue. Focal necrotic zones were evident adjacent to freely migrating plerocercoids (Fig. 17 and 18). Pyknotic nuclei were present in cavities between plerocercoids and liver parenchyma. There was no host cellular response associated with early tissue damage.

Initial host response consisted of macrophages and polymorphonuclear leucocytes (PMN) appearing at necrotic zones. Fibroblasts then surrounded the plerocercoid in a thin one cell layer. Often, some necrotic tissue, macrophages and PMN were enclosed within the developing fibrous capsule and stained densely eosinophilic. Encapsulation continued until plerocercoids were contained by concentric layers of dense, acellular fibrous tissue, comprised mainly of collagen. Concentrations of leucocytes, including eosinophilic granulocytes (EG), PMN, macrophages and a few lymphocytes surrounded the periphery of the capsule and extended slightly into the liver parenchyma. Dead plerocercoids were recognized by an eosinophilic, amorphous centre encompassed by a relatively cellular fibrous capsule. In some cases, capsules containg dead plerocercoids were invaded with leucocytes and a few erythrocytes. Live, moribund and dead plerocercoids were found in the liver of walleye in age classes 0 to 7+. However, more plerocercoids were judged to be dead than

Figs. 17 - 20. Fig. 17. Zone of necrotic hepatocytes (nl) surrounding a live plerocercoid (pl) invading the liver (li) of an age 6 walleye. (p), pancreas. Lillies A&B, X 64. Fig. 18. Extensive hepatic necrosis (nl) adjacent to a live plerocercoid (pl) invading the liver of a YOY walleye. Lillies A&B, X 18. Fig. 19. Migrating plerocercoid (pl) in the mesenteries of a young-of-the-year walleye. (s), spleen; (arrow), initial inflammatory response. Lillies A&B, X 12.4. Fig. 20. Concentration of inflammatory cells (arrow) adjacent to dead, encapsulated plerocercoids in an age 5 walleye. (cw), capsule wall. Lillies A&B, X 64.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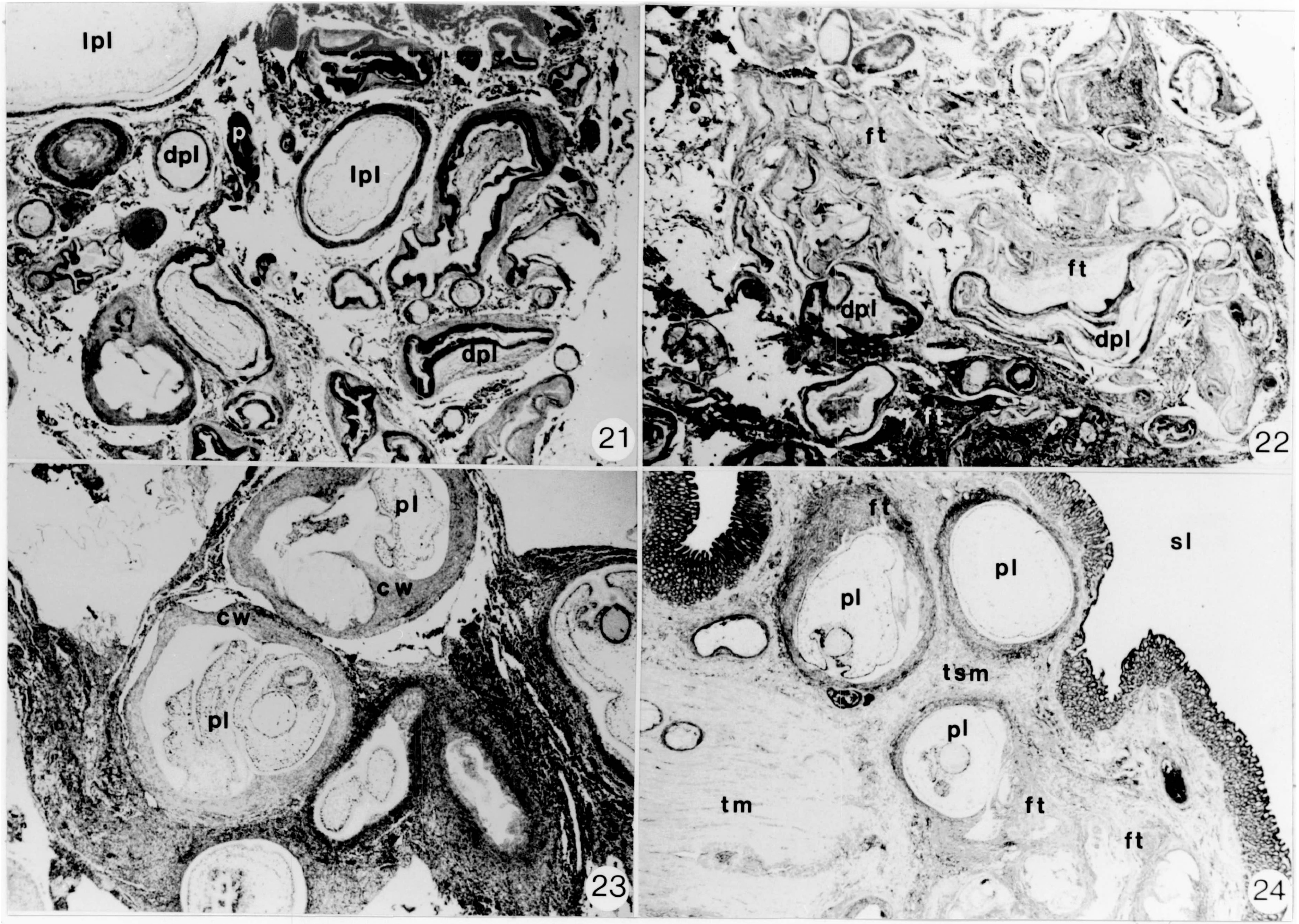
alive in walleye age 3 and older.

Mesenteries - Freely migrating plerocercoids in the mesenteries of walleye initially elicited little host response (Fig 19). Host reaction and capsule formation was identical to the process that occurred in the liver. Extensive focal conentrations of inflammatory cells, including EG, PMN, macrophages and lymphocytes surrounded the capsule (Fig. 20). Eosinophilic granulocytes were the most conspicuous leucocyte around encapsulated plerocercoids.

Plerocercoids in the mesenteries were individually encapsulated. Capsules were a maximum of 90 microns thick. Severe fibrosis of the mesenteries was evident where many plerocercoids had been encapsulated and overcome. The mesenteries eventually became an organized mass of dense fibrous tissue. Live, moribund and dead plerocercoids were present in all age classes of walleye, however, the proportion and concentration of dead plerocercoids increased in older walleye (Figs. 21 and 22). In yellow perch, the reaction to migrating plerocercoids invading the mesenteries was similar to that noted in walleye. However, the fibrous capsules were much more extensive, being a maximum thickness of 290 microns (Fig. 23). Each capsule was discrete and not aggregated into a fibrous mass. Most encapsulated plerocercoids in yellow perch were alive even in fish 7 to 9 years of age.

Gastro-intestinal tract - Some plerocercoids in walleye

Figs. 21 - 24. Fig. 21. Live (lpl) and dead (dpl) encapsulated plerocercoids in the mesenteries of an age 6 walleye. (p), pancreas. Lillies A&B, X 8. Fig. 22. Many dead plerocercoids (dpl) accumulating in the mesenteries of an age 4 walleye causing the proliferation of fibrous tissue (ft). Lillies A&B, X 7.6. Fig. 23. Thick capsule wall (cw) encompassing live plerocerocoids (pl) in the mesenteries of an age 9 yellow perch. Lillies A&B, X 8. Fig. 24. Encapsulated plerocercoids (pl) in the tunica submucosa (tsm) of an age 6 walleye. (ft), fibrous tissue; (sl), stomach lumen; (tm) tunica muscularis. Lillies A&B, X 7.6.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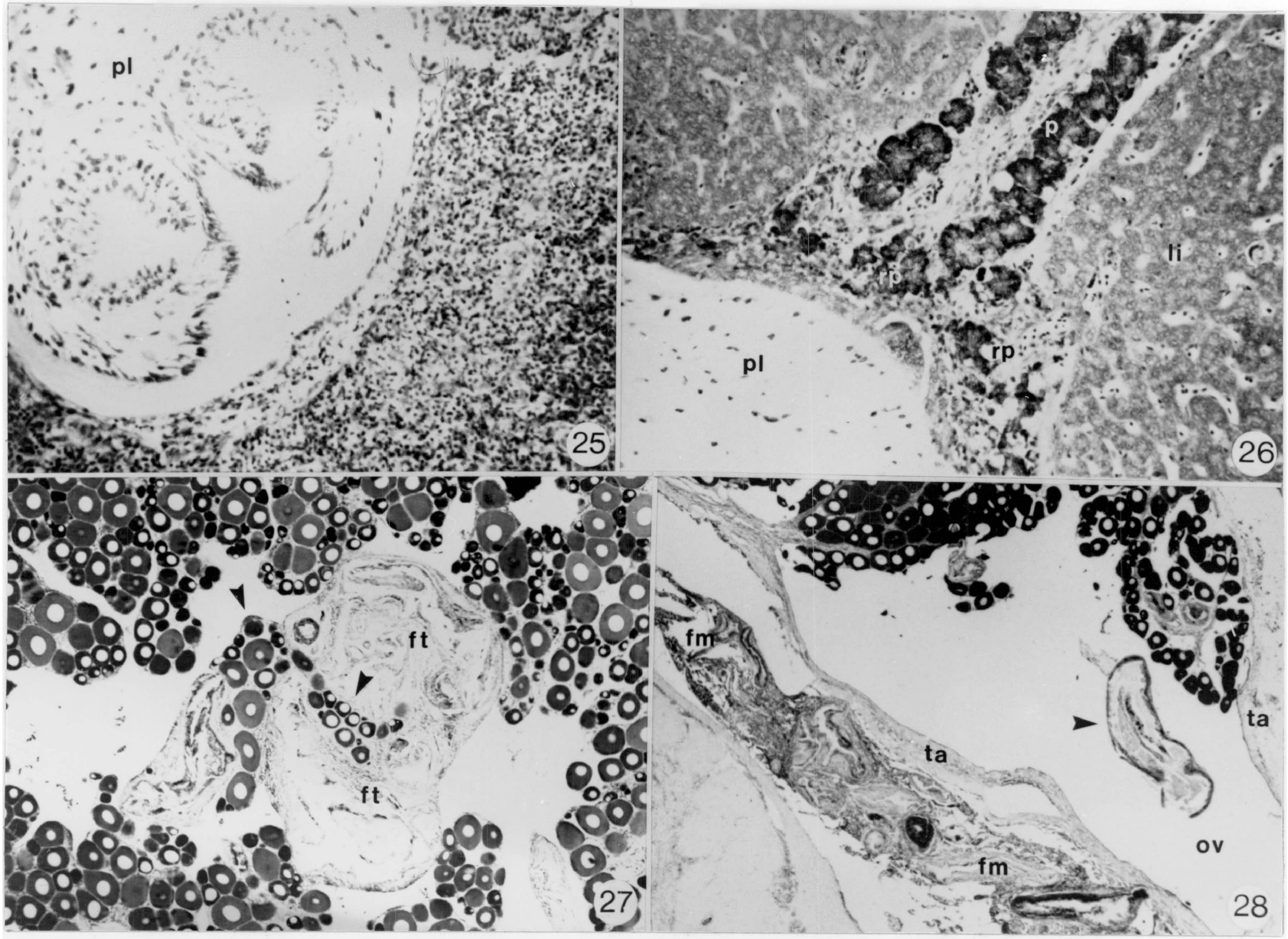
and yellow perch were arrested during their migration from the lumen of the stomach to parenteral sites. Encapsulated plerocercoids were found predominantly in the tunica submucosa, and to lesser degree, the tunica muscularis of the stomach (Fig. 24). In some walleye, when many plerocercoids were encapsulated, fibrous connective tissue replaced a large portion of the normal cell complement of the tunica submucosa, resulting in fibrosis of the stomach wall. Concentrations of inflammatory cells surrounded each capsule. Petechial haemorrhages were occasionly found near migrating plerocercoids.

Spleen and Pancreas - Plerocercoids in the spleen of walleye were encapsaulted by thin, dense layers of fibroblasts. Concentrations of inflammatory cells were not evident. Plerocercoids caused only a minor displacement and compression of spleenic pulp (Fig. 25).

Wandering plerocercoids were responsible for compression and rupture of pancreatic acinar cells (Fig. 26). Small extracellular concentrations of zymogen granules were common next to ruptured cells. Focal necrotic zones of pancreatic tissue were evident. Macrophages, PMN and EG were present at necrotic zones.

Gonads - In male walleye, seminiferous tubules were ruptured by migrating plerocercoids. Signs of a general inflammatory response were not observed but some encapsulated plerocercoids were seen. In female walleye, plerocercoids invading ovarian stroma caused localized

Figs. 25 - 28. Fig. 25. A migrating plerocercoid (pl) invading the spleen and the minor associated inflammatory response in an age 1 walleye. Lillies A&B, X 64. Fig. 26. Ruptured pancreatic acinar cells (rp) adjacent to a migrating plerocercoid (pl) in the liver of an age 2 walleye. (p), normal pancreatic cells. Lillies A&B, X 64. Fig. 27. Oocytes (arrows) caught in the fibrous tissue (ft) encompassing some dead plerocercoids in the ovary of an age 4 walleye. Lillies A&B, X 20. Fig. 28. A dead encapsulated plerocercoid (arrow) in the lumen of the oviduct, and fibrosed mesenteries (fm) in an age 4 walleye. (ta), tunica albuginea of ovary and oviduct. Lillies A&B, X 7.2.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compression of oocytes. Around free plerocercoids were a few fibroblasts, PMN, EG, and macrophages. As in other areas, when ecapsulation was complete, leucocytes surrounded the periphery of the capsule. Occasionally, a few oocytes were found encompassed in the fibrous tissue comprising the capsules (Fig. 27). Encapsulated plerocercoids were also found in the lumen of the anterior oviduct (Fig. 28). Plerocercoids did not invade the gonads in large numbers and the inflammatory response in the testes and ovaries was not extensive.

In many walleye, the mesenteries joining the posterior intestine and posterior gonads were invaded by many migrating plerocercoids. Severe fibrosis was evident and this region was often compacted into one fibrous mass. The oviduct and ductus deferens were also included in this fibrous mass. Encapsulated plerocercoids surrounded the oviduct and ductus deferens, however there was no direct evidence that blockage and/or constriction of gamete passage was occurring.

DISCUSSION

Biology of P. amblopitis

The general level of infection of *P. amblopitis* plerocercoids in walleye and yellow perch from Lake of the Woods has increased substantially over the last 2 decades. In the present study 100% of the age 1 and older walleye were infected (mean intensity = 73) and 74% of the age 1 and older yellow perch (mean intensity = 6) harboured parenteral plerocercoids. Dechtiar (1972) examined both percids from Lake of the Woods from 1963 - 66 and found only 38% of the walleye and 24% of the yellow perch to be infected, and no fish had more than 10 plerocercoids. Smallmouth bass, the definitive host of *P. amblopitis*, probably are more widely dispersed in Lake of the Woods than in previous years (V. Macins pers. comm.). This species is probably the major definitive host in Lake of the Woods and its increased numbers and distribution may account for the increased level of infection in the two percid accidental hosts.

In other ecosystems where walleye and yellow perch harboured *P. amblopitis* plerocercoids, yellow perch was the species most frequently infected (Table 26). For example, Fischthal (1947) reported that only 1 of 118 walleye sampled from northern Wisconsin lakes had parenteral plerocercoids whereas 40 of 114 (28%) of the yellow perch from the same lakes were infected. In Lake of the Woods the reverse was seen and in general, walleye were 10 times more

TABLE 26. A bibliographic summary of parenteral *P. amblopliti*s in North American fresh water fish

Fish species		Authority
Rock bass	*Ambloplites rupestris*	Pearse (1924); Hunter and Hunter (1929); Van Cleave and Mueller (1934); Bangham and Hunter (1939); Fischthal (1947); Bangham (1955); Freze (1965)
Smallmouth bass	*Micropterus dolomieui*	Cooper (1915); Pearse (1924); Van Cleave and Mueller (1934); Bangham and Hunter (1939); Bangham (1941a; 1941b); Fischthal 1947); Bangham (1955); Freze (1965); Dechtiar (1972)
Largemouth bass	*Micropterus salmoides*	Pearse (1924); Hunter and Hunter (1929); Bangham and Hunter (1939); Bangham (1941a); Fischthal (1947); Bangham (1955); Freze (1965)
Pumpkinseed	*Lepomis gibbosus*	Van Cleave and Mueller (1934); Bangham and Hunter (1939); Bangham (1941a; 1941b); Fischthal (1947); Bangham (1955); Freze (1965); Dechtiar (1972)

TABLE 26. (continued)

Fish species		Authority
Green sunfish	Lepomis cyanellus	Bangham (1941a); Fischthal (1947); Freze (1965); Hoffman (1967); Harley and Keefe (1970); McDaniel and Bailey (1974)
Longear sunfish	Lepomis megalotis	Bangham (1941a); Freze (1965); Hoffman (1967); Harley and Keefe (1970); McDaniel and Bailey (1974)
Bluegill	Lepomis macrochirus	Pearse (1924); Bangham and Hunter (1939); Bangham (1941a); Fischthal (1947); Freze (1965); Hoffman (1967); Harley and Keefe (1970); McDaniel and Bailey (1974)
Redear sunfish	Lepomis microlophus	Hoffman (1967); Harley and Keefe (1970)
Orange spotted sunfish	Lepomis humilis	Hoffman(1967)
White crappie	Pomoxis annularis	Bangham (1941a); Freze (1965); Hoffman (1967); Harley (1977)
Black crappie	Poxomis nigromaculatus	Fischthal (1947); Freze (1965); Hoffman (1967); Dechtiar (1972)

TABLE 26. (continued)

Flier	*Centrarchus macropterus*	Hoffman (1967)
Yellow perch	*Perca flavescens*	Cooper (1915); Pearse (1924); Hunter and Hunter (1929); Van Cleave and Mueller (1934); Bangham and Hunter (1939); Bangham (1941b); Fischthal (1947); Freze (1965); Hoffman (1967); Tedla and Fernando (1970); Dechtiar (1972)
Sauger	*Stizostedion canadense*	Dechtiar (1972)
Walleye	*Stizostedion vitreum vitreum*	Bangham and Hunter (1939); Fischthal (1947); Freze (1965); Dechtiar(1972); Sutherland and Holloway (1979)
Blue walleye	*Stizostedion vitreum glaucum*	Bangham and Hunter (1939); Freze (1965)
Tesselated darter	*Etheostoma olmstedi*	Van Cleave and Mueller (1934)
Fantail darter	*Etheostoma flabellare*	Fischthal (1947)
Johnny darter	*Etheostoma nigrum*	Freze (1965); Hoffman (1967)
Brown bullhead	*Ictalurus nebulosus*	Pearse (1924); Van Cleave and Mueller (1934); Bangham (1941a; 1941b); Fischthal (1947); Bangham (1955); Freze (1965); Dechtiar (1972)

TABLE 26. (continued)

Black bullhead	*Ictalurus melas*	Bangham and Hunter (1939); Bangham (1941a); Freze (1965)
Yellow bullhead	*Ictalurus natalis*	Pearse (1924); Fischthal (1947); Freze (1965)
Channel catfish	*Ictalurus punctatus*	Pearse (1924); Van Cleave and Mueller (1934); Bangham (1941a)
Stonecat	*Noturus flavus*	Bangham and Hunter (1939); Freze (1965)
Tadpole madtom	*Noturus gyrinus*	Bangham (1941a); Freze (1965)
Flathead catfish	*Pylodictis olivaris*	Hoffman (1967)
Rainbow trout	*Salmo gairdneri*	Becker and Brunson (1968)
Cutthroat trout	*Salmo clarki*	Becker and Brunson (1968)
Brook trout	*Salvelinus fontinalis*	MacLulich (1943); Becker and Brunson (1968)
Lake trout	*Salvelinus namaycush*	MacLulich (1943); Becker and Brunson (1968)
Coho salmon	*Oncorhynchus kisutch*	Becker and Brunson (1968)
Cisco	*Coregonus artedii*	Hoffman (1967)
Chain pickerel	*Exos niger*	Pearse (1924); Van Cleave and Mueller (1934); Hunter and Rankin (1940); Freze (1965)

TABLE 26. (continued)

Grass pickerel	*Esox americanus vermiculatus*	Hunter and Rankin (1940)
Northern pike	*Esox lucius*	Hunter and Rankin (1940); Fischthal (1947); Freze (1965)
Muskellunge	*Esox masquinongy*	Fischthal (1947); Freze (1965)
Emerald shiner	*Notropis atherinoides*	Pearse (1924); Bangham and Hunter (1939); Freze (1965)
Spottail shiner	*Notropis hudsonius*	Bangham and Hunter (1939); Freze (1965)
Creek chub	*Semotilus atromaculatus*	Fischthal (1950); Freze (1965); Fischer and Freeman (1973)
Sucker	*Catastomus* spp.	Pearse (1924)
Lake chub sucker	*Erimyzon sucetta*	Hoffman (1967)
Smallmouth buffalo	*Ictiobus bubalus*	Hoffman (1967)
Mottled sculpin	*Cottus bairdi*	Bangham and Hunter (1939); Freze (1965); Dechtiar (1972)
Prickly sculpin	*Cottus asper*	Becker and Brunson (1968)
Longnose gar	*Lepiosteus osseus*	Pearse (1924); Bangham and Hunter (1939); Freze (1965)
Shortnose gar	*Lepiosteus platastomus*	Hoffman (1967)

TABLE 26. (continued)

Yellow bass	*Morone mississippiensis*	Hoffman (1967)
White bass	*Morone chrysops*	Pearse (1924); Bangham and Hunter (1939); Bangham (1955)
Brook stickleback	*Culaea inconstans*	Dechtiar (1972)
Banded killifish	*Fundulus diaphanus*	Pearse (1924); Hunter and Hunter (1929)
Brook silverside	*Labidesthis sicculus*	Bangham and Hunter (1939); Freze (1965)
Burbot	*Lota lota*	Hoffman (1967)
Bowfin	*Amia calva*	Pearse (1924); Bangham and Hunter (1939)
Pirate perch	*Aphredoderus sayanus*	Hoffman (1967)
Freshwater drum	*Aplodinotus grunniens*	Pearse (1924)

heavily infected than yellow perch. Since walleye is a top predator, a bio-accumulation of plerocercoids could result in the 100% infection level and the relatively high intensities found in this percid in Lake of the Woods. Walleye in Lake of the Woods would be constantly preying on infected forage fish whereas in other ecosystems, infected forage fish must be rare in the diet of walleye.

Plerocercoid intensity was related to age of the host but varied with species. In walleye, the number of parenteral plerocercoids increased to a maximum mean of 171 in age class 5 then decreased significantly in older fish. However, in yellow perch, intensity increased gradually until age 4 then more than doubled to a mean of 20 in the 5+ age class. Although smallmouth bass is an intermediate, as well as a definitive host, the number of plerocercoids in this species also increased with age then declined in older fish as was observed here in walleye. Hunter and Hunninen (1934) found that intensity increased to a maximum mean of 65 in bass 7 to 9 years of age, then declined in older fish. Fischer (1972) noted that smallmouth bass, 23 to 28 cm in length, harboured a mean of 122 plerocercoids but fish larger than 28 cm harboured a mean of only 58 plerocercoids. Similarly, Morrison (1957) reported that smallmouth bass 24 to 33 cm in length harboured the greatest mean number of plerocercoids although fish up to 50 cm had been sampled. The population dynamics of plerocercoids is similar in walleye and smallmouth bass although the former is an accidental, and the latter, the natural host.

A number of factors may influence the decline in the number of plerocercoids found in older walleye and smallmouth bass. First, the plerocercoids may reach their maximum life span so that in older fish, natural mortality of plerocercoids is exceeding recruitment. Although the life span of P. amblopliti s plerocercoids has not been determined, Bailey (1984) suggested that plerocercoid longevity may have contributed to the apparent increase in intensity with increasing age of bluegill (Lepomis macrochirus). The plerocercoids of Ligula intestinalis L., 1758 and Schistocephalus solidus Muller, 1776 have been reported to live as long as their respective hosts (Arme and Owen 1968; Pennycuick 1971; Sweeting 1976). Also, Rosen and Dick (1984) found that plerocerocoids of Triaenophorous crassus Forel, 1880 can live more than 3 years in whitefish. It is possible then, that P. ambloplitis plerocercoids could live as long as walleye, smallmouth bass and/or yellow perch. In yellow perch where there was no decline in intensity with increasing age, the plerocercoids may survive most of their potential life span. In walleye and smallmouth bass roughly the same age as yellow perch, the decline in plerocercoid numbers indicates that they are not as long-lived in these species. In fact, histological examimation revealed dead plerocercoids in YOY walleye which suggests that at least some plerocercoids are relatively short-lived. It appears that plerocercoids in walleye and probably smallmouth bass are not realizing their potential life span. The decline in the number of live plerocercoids recovered from older walleye and smallmouth bass most likely can not be attributed to natural mortality of the parasite.

A second hypothesis that might explain the presence of fewer plerocercoids in older walleye and smallmouth bass is that the most heavily infected fish die. Heavy infections of larval cestodes in fish have been cited as a cause of host mortality. Holloway (1984) proposed that mortality of young ninespine sticklebacks in Matamek Lake, Quebec was a result of severe infections of *S. solidus*. Plerocercoids of *Diphyllobothrium* have been noted to cause mortality in brown trout, rainbow trout (*Salmo gairdneri*) and brook trout (*Salvelinus fontinalis*) (Fraser 1960; Hoffman and Dunbar 1961). Mortality of Arctic char (*Salvelinus alpinus*) was also attributed to heavy infections of *D. dentriticum* Nitzsch, 1824 (Henricson 1978). During the present study, there was no evidence that severe *P. ambloplitis* infections caused mortality of walleye. In fact, there were older and larger walleye in the population which had infections that visually appeared to be severe, but when examined in detail, harboured few live plerocercoids. This suggests that heavily infected fish are ot being lost from the population. Rather, it appears that many plerocercoids are being killed by the host.

Finally, the host's defense mechanisms may be more competent with age and continuous parasitic challenge, resulting in the decline in the number of live plerocercoids found in older walleye and smallmouth bass. In fact, Hunter and Hunninen (1934) proposed that an age resistance may explain the decline in the number of plerocercoids found in older smallmouth bass. Finn and Nielson (1971) also suggested that the age and size of a fish may have some effect on the host's inflammatory response. The fact there were some older walleye, examined during the present study, with apparently severe infections but which actually had few live plerocercoids provides some evidence for this hypothesis. But, the presence of moribund and dead plerocercoids in YOY and young walleye suggests that some plerocercoids succumb to the host's defense mechanisms shortly after parenteral invasion. However, immuno-competence may be age dependent in fish which could account for the rapid decline in numbers of plerocercoids found in older walleye and smallmouth bass. Bauer (1984) reported that in some instances of monogenean infections the immune response of fish was greater as the parasite burden increased. The immune system of older walleye and smallmouth bass may be responding to the heavy plerocercoid loads found in these species. The defense mechanisms of yellow perch may be less effective or not stimulated as intensely as in the other species, allowing the plerocercoids to live longer.

Not all organs were invaded equally by plerocercoids. The liver was the first organ of YOY walleye and YOY yellow perch to be invaded by penetrating plerocercoids. In walleye, plerocercoids continued to accumulate in the liver until age 2 (mean = 13), but with increasing age of fish there was a significant decline in the importance of the liver as a site of infection. Conversely, the mean number of plerocercoids found in the liver of yellow perch continued to increase with increasing age. The decline in the mean number of plerocercoids recovered from the liver of walleye may be a result of plerocercoid mortality or the migration of plerocercoids from the liver to another site. Histological examination revealed that plerocercoids were in the liver of age 3 and older walleye, however the majority were moribund or dead. Therefore, in age 3 and older walleye invasion of plerocercoids into the liver is exceeded by plerocercoid mortality. Some emigration may be occurring but it would be very difficult to assess.

Cooper (1915) also found the liver of YOY smallmouth bass to be the first organ to harbour penetrating plerocercoids. Hunter and Hunninen (1934) reported that the liver of smallmouth bass accumulated more plerocercoids as the fish grew. In contrast, Fischer (1972) noted a decline in the relative percentage and the mean number of plerocercoids recovered from the liver of smallmouth bass with increasing size. Fischer (1972) offered no explanation as to why that might be, however it appears comparable to the situation in walleye.

The mesenteries rapidly became the most important site of infection in accidental and natural hosts. The mesenteries harboured the majority (up to 80%) of all parenteral plerocercoids in walleye age classes 1 to 7+. However, there was a decline in the mean number of plerocercoids recovered from walleye in age classes 6 and 7+. The mesenteries of young yellow perch were not important as a site of infection but in age class 5+ the mesenteries contained the majority (69%) of all parenteral plerocercoids. There was not the same decline in the mean number of plerocercoids found in the mesenteries in older yellow perch as was evident in walleye. Emigration could not account for the decline in the mean number of plerocercoids found in the mesenteries of older walleye. The other visceral organs were not increasing in importance as a site of infection as would be evident if plerocercoids were immigrating. Nor were plerocercoids migrating back to the intestine to mature. Therefore, plerocercoid death must be responsible for the decline in the mean number of live plerocercoids recovered from the mesenteries of older walleye. The mesenteries of older walleye harboured many encapsulated plerocercoids, and histological examination determined that the majority were, in fact dead.

Similarly, Fischer (1972) found fewer plerocercoids in the mesenteries of older and larger smallmouth bass than in younger fish. The mesenteries of smallmouth bass fry accounted for 54% of all parenteral plerocercoids and only 36% in fish 28 cm and larger. The mean number of plerocercoids in the mesenteries decreased with increasing size of smallmouth bass. Maximum mean number was 53 per fish in the 23 cm to 28 cm size group but was only 21 for fish greater than 28 cm. Some of the plerocercoids may have been migrating to the gonads or back to the intestine, depending on the season sampled. There may also have been high plerocercoid mortality as noted in walleye.

The spleen, gallbladder and kidney of walleye and yellow perch were rarely invaded by plerocercoids. The mean number of plerocercoids in these organs rarely exceeded 1 per fish. Of the three organs, the spleen was the most commonly infected, containing approximately 2.5% of all plerocercoids in all age classes of walleye and yellow perch. Cooper (1915) and Fischer (1972) also reported that a plerocercoid invading the kidney or gallbladder of smallmouth bass was a relatively rare occurrence. Hunter and Hunninen (1934) found that the spleen of smallmouth bass continued to accumulate plerocercoids with increasing age. In contrast, Fischer (1972) reported that the spleen contained a relatively stable percentage (3.3 to 4.8%) of parenteral plerocercoids in all size classes of smallmouth bass. It is apparent that the spleen, gallbladder and kidney represent relatively unimportant areas for a *P. ambloplitis* plerocercoid infection, at least in walleye and yellow perch.

When a parasite invades an organ there may be a partial reduction in, or the complete loss of function of that organ. The gonads represent an area of special interest. Severe ovarian infections could cause decreased reproductive potential and the demise of future population levels. The gonads of older and larger smallmouth bass have been reported to harbour the majority of all parenteral plerocercoids (Hunter and Hunninen 1934; Fischer 1972). Hunter and Hunninen (1934) found that the gonads of smallmouth bass contained 19 to 40 plerocercoids, accounting for 70% to 80% of all parenteral plerocercoids. Similarly, Fischer (1972) reported that the gonads of smallmouth bass, 23 to 28 cm, contained a mean of 39 plerocercoids and accounted for 42% of the total infection. Smallmouth bass apparently have been rendered sterile by heavy plerocercoids infestations (Moore 1925; Bangham 1927a; Bangham 1927b).

The gonads of walleye harboured relatively few plerocercoids (about 5% in all age classes) in comparison to other visceral organs. Similarly, the gonads of yellow perch were rarely invaded by parenteral plerocercoids. In contrast, Dechtiar (1972) reported that the ovaries, "in particular", contained plerocercoids in infected walleye. The estimated fecundity of walleye from Lake of the Woods indicated that egg production has not been adversely affected. The present study estimated fecundity to be 63,300 eggs per kg of female regardless of plerocercoid intensity. Carlander (1945) reported that walleye from Lake of the Woods produced approximately 50,000 eggs per kg of female. It appears that fecundity may have even increased from the time of Carlander's (1945) study. The present fecundity estimate is also within the range reported by other authors (Preigel 1969a; Wolfert 1969; Serns 1982; Baccante unpubl.) At present there is not a problem with the numbers of plerocercoids invading the gonads, especially the ovaries, of walleye.

In walleye, the severity of mesenteric fibrosis in the oviduct region may be cause for concern. There was extensive mesenteric fibrosis along the posterior ovaries and oviduct as well as fibrous capsules present in the lumen of the anterior oviduct. The constriction and/or blockage of the oviduct as a result of the fibrous reaction could impede the passage of mature ova. If the eggs can not be passed then the fish is rendered functionally sterile. Blockage of the oviduct may account for the presence of 2 female walleye, captured during early July, resorbing their entire complement of eggs. Fibrosis of the mesenteries the region of the lower intestine and posterior gonads is cause for concern because the majority of the walleye had an accumulation of encapsulated plerocercoids in this region.

Young-of-the-year yellow perch from Lake of the Woods probably became infected by preying on copepods. Copepods (*Cyclops prasinus* , *C. vulgaris* , *Macrocyclops annulicornis* , *Eucyclops agilis* , *C. vernalis*) are the only experimentally proven intermediate hosts of *P. amblopIitis* (Hunter 1928; Hunter and Hunter 1929; Fischer

1972). Bangham (1925) reported that *Hyalella azteca* was naturally infected with *P. ambloplitis* , however, Fischer (1972) could not experimentally duplicate the infection. Therefore, it appears unlikely that amphipods serve as an intermediate host for *P. ambloplitis* . Weber and Les (1982) reported that 94% of total food volume consumed by YOY yellow perch consisted of copepods and cladocerans. In the present study, copepods were rare in the stomachs of YOY yellow perch during August and September but higher water temperatures at that time of year may have lowered gastric evacuation time so that copepods may have been digested at the time of examination.

Forage fish probably were more important than copepods in transmitting plerocercoids to older yellow perch. During the present study, insect larvae and crustaceans, other than copepods, were the most important prey items of age 1 and older yellow perch. However, yellow perch did feed on fish and were periodically cannibalistic during the summer months. Cannibalism probably represents the major method of plerocercoid recruitment by older yellow perch. The minor importance of fish in the diet of yellow perch may explain why they are not as heavily infected with plerocercoids as walleye.

Yellow perch have been reported to change their diet with increasing size. Young-of-the-year yellow perch begin feeding at 6 to 7 mm in length and feed on copepods (Siefert 1972). Small yellow perch, up to 15 cm, feed primarily on invertebrates including amphipods, cladocerans, insects and crayfish (Clady 1974; Kelso and Ward 1977; Elrod et al. 1981; Hubert and Sandheinrich 1983). Yellow perch larger than 15 cm prey to a larger extent on fish. Cannibalism on their own young-of-the-year is a relatively common occurrence (Clady 1974; Elrod et al. 1981). Clady (1974) reported that 56% of total food volume of adult yellow perch (from April to August) was composed of fish of which young perch were the most common of identifiable remains. Elrod et al. (1981) and Kelso and Ward (1977) also found that adult yellow perch were primarily piscivorous during July and August especially on young perch and brook sticklebacks. The shift in diet of yellow perch, from one primarily consisting of invertebrates to one primarily composed of fish, would account for the sharp increase in plerocercoid intensity in the 5+ age class.

Walleye in all age classes, 0 to 7+, became infected by preying on fish. Yellow perch was the most important fish in transmitting plerocercoids to walleye in Lake of the Woods. Yellow perch were the most frequently and heavily infected forage fish examined during the present study and were commonly found in the stomachs of walleye. Although YOY walleye begin feeding on copepods and cladocerans when they are 9 mm in length (Bulkley et al. 1976), Colby et al. (1979) reported that walleye could be piscivorous when they reached 30 mm in length. In Lake Winnebago, YOY walleye less than 50 mm were already consuming fish, and by 76 mm, 96%

had fish remains in their stomachs (Preigel 1969b). During the present study YOY walleye from Lake of the Woods were primarily piscivorous in July when they were a mean of 65 mm in length. However, YOY walleye were not infected with plerocercoids until they were 93 mm in length (in 1983). Young-of-the-year yellow perch was the major identifiable food item of YOY walleye at that time. Yellow perch, especially the YOY, were also the most important fish prey item found in the stomachs of age 1 and older walleye.

Colby et al (1979) reported that YOY yellow perch, when available, were the preferred prey of walleye. Swenson and Smith (1976), studying the food habits of walleye from Lake of the Woods, found that yellow perch were the dominant forage species from June to September. However, many other species of fish are also utilized as prey by walleye when necessary (Swenson and Smith 1976; Colby et al 1979). A diversified diet would increase the number of plerocercoids found in walleye when they were not preying on yellow perch. These other infected forage fish would be of minor importance in transmitting plerocercoids to walleye in Lake of the Woods.

Many species of fish have been reported to harbour P. ambloplitis plerocercoids (Table 26). In fact, during the present study logperch and ninespine sticklebacks were found to be infected with plerocercoids which constitute new host records. But only those in which the plerocercoid could survive for an extended period of time would be important in transferring the parasite to walleye. In some experimentally infected fish (northern redbelly dace (*Phoxinus eos*), pearl dace (*Semotilus margarita*), golden shiner (*Notemigonus crysoleucas*), and creek chub (*Semotilus atromaculatus*)), plerocercoids were moribund within 2 weeks post-infection (Fischer 1972). Sticklebacks from Lake of the Woods were found to be infected in 1982 and 1983 but not before August although, Scott and Crossman (1973) reported that these fish can live for more than 1 year. Sticklebacks may be another example of an intermediate host in which *P. amblоplitis* plerocercoids can survive for only a short period of time. Therefore only a few species of fish appear to be important in the life history of *P. amblоplitis* . In Lake of the Woods, species of centrarchids and ictalurids would also be important in transmitting plerocercoids to walleye because live plerocercoids were recovered from these fish at all times during the sampling period.

Young-of-the-year walleye and YOY yellow perch were not found to harbour plerocercoids until August. The almost simultaneous appearance of plerocercoids in the YOY walleye and yellow perch does not negate the importance of yellow perch as a vehicle of transmission. Plerocercoids can penetrate the stomach wall very quickly. Fischer (1972) reported that in an experimental feeding of infected copepods, plerocercoids were present on the liver of the recipient fish only 7 hours post-exposure. This short penetration time means the almost simultaneous appearance of plerocercoids in YOY walleye and yellow perch could be expected. It also suggests that plerocerocoids are not available in copepods prior to August.

The significance of plerocercoids free in the peritoneal cavity has not been previously considered. In the present study, it has been proposed that plerocercoids free in the peritoneal cavity represent recently acquired larvae. An assessment of how and when recruitment of the parasite occurs may then be determined.

There was a distinct seasonality in recruitment of plerocercoids by age 1 and older walleye whereas in age 1 and older yellow perch there was little seasonal variation. A minor peak in the mean number of plerocercoids free in the peritoneal cavity of age 1 and older yellow perch was apparent during August. This correlates with the time yellow perch were most cannibalistic. In walleye, there was a significant increase in the mean number of free plerocercoids from May to the early summer months with another increase from August to September. There was then a significant decline in the mean number of free plerocercoids between September and November. A seasonal shift occurred in the diet of walleye corresponding with the increase in the mean number of plerocercoids free in the body cavity. In May, insect larvae were the dominant prey item. However, fish became increasingly more important as the summer progressed, until by September, 93% of total food volume consisted of yellow perch. This evidence supports the hypothesis that walleye obtain the majority of their plerocercoids from yellow perch. The presence of few plerocercoids free in the body cavity during November suggests transmission of plerocercoids is not important during the winter months. Although stomach samples were not collected during November, decreased transmission of plerocercoids probably reflects a decline in food consumption by walleye at this time of year.

Walleye and yellow perch in Lake of the Woods were not suitable definitive hosts for _P. amblopliti_s . Only one segmenting, but non-gravid _P. amblopliti_s was recovered from the intestine of a walleye. Many species of fish have been reported as suitable definitive hosts including walleye and yellow perch (Table 27), but some species likely represent rare occurrences or even cases of mis-identification. Sutherland and Holloway (1979) reported an enteral specimen from a shortnose gar (_Lepisosteus platastomus_) but examination of the specimen in our laboratory revealed that it was wrongly identified.

During the present study, only smallmouth bass were found to harbour mature and gravid _P. ambloplitis_ . Dechtiar (1972) also found smallmouth bass to be the only species to harbour enteral _P. ambloplitis_ in Lake of the Woods. Gravid worms were found in smallmouth bass from late June to early August during 1982 and 1983. In other ecosystems, largemouth bass have been responsible for maintaining the life cycle of _P. ambloplitis_ (Eure 1976).

TABLE 27. A bibliographic summary of enteral _P. amblopl_itis in North American freshwater fish

Fish species		Authority
Rock bass	_Ambloplites rupestris_	Leidy (1887); Pearse (1924); Van Cleave and Mueller (1934); Bangham and Hunter (1939); Freze (1965); Hoffman (1967)
Smallmouth bass	_Micropterus dolomieui_	Cooper (1915); Pearse (1924); Bangham and Hunter (1939); Bangham (1941a); Freze (1965); Hoffman (1967); Dechtiar (1972); Fischer (1972)
Largemouth bass	_Micropterus salmoides_	Pearse (1924); Van Cleave and Mueller (1934); Bangham and Hunter (1939); Freze (1965); Hoffman (1967)
Pumpkinseed	_Lepomis gibbosus_	Hoffman (1967)
Warmouth	_Lepomis gulosus_	Hoffman (1967)
Walleye	_Stizostedion vitreum vitreum_	Hoffman (1967)
Blue walleye	_Stizostedion vitreum glaucum_	Bangham and Hunter (1939); Hoffman (1967)
Yellow perch	_Perca flavescens_	Bangham (1941b); Freze (1965); Hoffman (1967); Tedla and Fernando (1970)
Johnny darter	_Etheostoma nigrum_	Hoffman (1967)

TABLE 27. (continued)

Fish species		Authority
Longnose gar	*Lepiosteus osseus*	Pearse (1924); Bangham and Hunter (1939)
Shortnose gar	*Lepisosteus platastomus*	Sutherland and Holloway (1979)
Chain pickerel	*Esox niger*	Hoffman (1967)
Redfin pickerel	*Esox americanus americanus*	Pearse (1924); Freze (1965); Hoffman (1967)
White bass	*Morone chrysops*	Pearse (1924); Hoffman (1967)
White perch	*Morone americana*	Hoffman (1967)
Brook trout	*Salvelinus fontinalis*	MacLulich (1943)
Lake trout	*Salvelinus namaycush*	MacLulich (1943)
Bowfin	*Amia calva*	Pearse (1924); Van Cleave and Mueller (1934); Freze (1965); Hoffman (1967)
Sucker	*Catastomus* spp.	Pearse (1924)
Creek chub	*Semotilus atromaculatus*	Fischthal (1950)
Brown bullhead	*Ictalurus nebulosus*	Hoffman (1967)
Freshwater drum	*Aplodinotus grunniens*	Hoffman (1967)

Also, rock bass have been cited as a suitable definitive host (Table 27), however it is not known if P. amblopitis could survive in a system where only rock bass resided. In Lake of the Woods, smallmouth bass likely represent the entire source of P. amblopitis present in the system. However, owing to small sample sizes it is not known if other centrarchids are a source for enteral P. amblopitis in Lake of the Woods.

Mature and gravid P. amblopitis were recovered only from mature smallmouth bass, during the present study. This is in agreement with the findings of Fischer and Freeman (1969) and Esch et al. (1975). In Lake of the Woods, the appearance of mature and gravid worms seemed to correspond to the onset of the spawning activity of its host. Esch et al. (1975) also reported the appearance of mature worms from smallmouth bass in Gull Lake at the temperature at which the smallmouth bass began to spawn. In view of this evidence, it seems likely that the maturation of P. amblopitis is more related to the physiological status of the host than to water temperature.

Histopathology

There were no gross physical deformities associated with heavy plerocercoid infections in walleye or yellow perch. However, Langlois (1936) reported that YOY smallmouth bass, 27 to 56 mm in length harbouring up to 67 plerocercoids per fish were characterized by a gross physical distention of the abdominal wall. Such heavy infections in YOY smallmouth bass were also responsible for host mortality (Langlois 1936). During the present study, individual YOY walleye harboured up to 85 plerocercoids (mean = 23, in September) but there was no associated deformity nor any evidence of mortality.

The inflammatory response and capsule formation around P. ambloplitis plerocercoids in walleye and yellow perch was similar to that seen in other infected fish species. Dense, layered, acellular capsules have been previously reported for P. ambloplitis plerocercoids infecting bluegills (Mitchill et al. 1983). Finn and Nielson (1971) reported that an intramuscular staphylococcal injection in young rainbow trout caused muscle necrosis within 3 hours post-injection (PI). The lesion was invaded by PMN within 12 to 24 hours and macrophages were present after 24 hours. Fibroblasts did not appear until 4 days PI with a major fibroplasia beginning by day 8 PI. By day 16, the major cellular component surrounding the lesion was the fibroblast. Sommerville (1981) also reported the appearance of macrophages within 24 hours and the onset of fibroplasia at approximately 8 days in species of flatfish experimentally infected with *Stephanochasmus baccatus* Nicoll, 1907. In contrast, whitefish experimentally infected with *T. crassus* reacted at a much slower rate (Rosen and Dick 1984). Haemorrhaging into lesions was the first apparent pathological change and occurred 17 days PI. Macrophages and PMN were also present at this time. Muscle necrosis was obvious only after 30 days PI and the proliferation of fibroblasts did not occur until 60 days PI. The schedule of encapsulation of *P. ambloplitis* plerocercoids in walleye is probably closer to what was reported by Sommervile (1981), and Finn and Nielson (1971). Some plerocercoids found in YOY walleye during September were already encapsulated and degenerating and they could only have been there for a maximum of 30 to 40 days. Since tissue damage was apparent only adajcent to freely migrating plerocercoids, rapid encapsulation would minimize pathological damage incurred by the host.

Yellow perch and walleye demonstrated differences in the intensity of host response as indicated by the thickness of the capsule surrounding plerocercoids. Sommerville (1981) found differences in the rate and intensity of host response to *S. baccatus* infecting 4 species of flatfish. It was suggested that the thicker capsules represented the most intense and prolonged reaction (Sommerville 1981). Therefore, yellow perch react more intensely to a plerocercoid insult than do walleye. The thick capsule surrounding plerocercoids in yellow perch may actually serve as protection, allowing for a prolonged life span of the parasite in this percid. However, the severe visceral fibrosis seen in walleye probably reflects the greater number of plerocercoids invading the viscera of this host rather than an unusually intense inflammatory response.

Host reaction, by walleye and yellow perch, to penetrating plerocercoids was characteristic of non-specific, chronic inflammation. Although lymphocytes were found in association with fibrous capsules they were not among the first cells to respond to insult. Sommerville (1981) also noted that lymphocytes were present only during the latter stages of the inflammatory response. Finn and Nielson (1971) reported that lymphocytes were a background type of cell and did not play a part in the inflammatory response. However, Hoole and Arme (1983) found an unknown leucocyte, tentatively identified as a lymphocyte, as part of the host response of roach fry (Rutilis rutilis) infected by L. intestinalis plerocercoids. There was a leucocyte attack on the tegument of the plerocercoid, but damage was minimal and the parasite was able to survive any initial damage. Although Hoole and Arme (1983) did not speculate on the function of these cells, lymphocytes in some species of fish have specific immune mechanisms (Ellis 1977). Bauer (1984) reported that the immunity manifested by fish in response to sublethal infections of monogeneans was not only by non-specific factors but also by specific antibodies. Maybe roach fry are eliciting a cell-mediated response to Ligula plerocercoids. Roberts, (1978) has suggested that a cell-mediated response may be important against parasitic infections.

Pathological changes in the tissues of walleye and yellow perch appeared to be independent of age. In all age classes, necrotic zones were localized, being associated with freely migrating plerocercoids. Once a plerocercoid was encapsulted, direct adverse effects on tissues were not observed. The liver incurred the most damage because of the number of plerocercoids invading this organ. Mitchill et al. (1983) reported a severe melanotic fibrosis of the liver in bluegills as a result of P. amblopitis plerocercoid migrations. In contrast, Esch and Huffines (1973) reported that the liver of smallmouth bass was the least damaged by migrating plerocercoids whereas the spleen suffered the greatest degree of pathological changes. In walleye, the other visceral organs did not appear to be as adversely affected as the liver. It appears the host response in individual organs of infected fish varies, and is species dependent.

The severe visceral fibrosis observed in walleye is also characteristic of heavy plerocercoid infections in smallmouth bass (Hoffman 1975). Sterility of smallmouth bass has been reported to occur as a result of these heavy plerocercoid infections (Moore 1925; Bangham 1927a; Bangham

1927b). In smallmouth bass, migrating plerocercoids caused fibrosis of ovarian tissue which apparently was the reason for sterility (Hoffman 1975). McCormick and Stokes (1982) reported that plerocercoids invading the ovary actually penetrated, and were responsible for, destroying individual oocytes. The same phenomenon was not observed in walleye. In general, the damage incurred by the ovaries of walleye as a result of migrating plerocercoids was minimal. However, fibrosis of the mesenteries surrounding the posterior ovary and oviduct may cause functional sterility in walleye. Constriction and/or blockage of the oviduct may occur, impeding the passing of ova. The presence of encapsulated plerocercoids in the lumen of the oviduct in walleye is supporting evidence for this hypothesis. Encapsulated plerocercoids in the lumen of the oviduct would create a physical barrier hindering the passage of eggs. Constriction of the oviduct would result from the extensive proliferation of fibrous tissue in that area. The oviducts of smallmouth bass were also marked by extensive scarring and "cysts" were frequently found in the lumen (Esch and Huffines 1973). These authors also suggested that extensive fibrosis in the oviduct region could prevent the passage of eggs. The damage to the testes of smallmouth bass was structural and Esch and Huffines (1973) estimated that 80% of the sperm producing tissue of young males could be destroyed by migrating plerocercoids. The few plerocercoids found in the testes of walleye could not be responsible for any extensive damage to testicular germ cells especially if encapsulation is relatively quick.

The introduction of smallmouth bass into Lake of the Woods has not yet had a wide-spread, detrimental affect on indigenous fish species, however, the potential exists. If intensities of *P. amblopltitis* plerocercoids infecting walleye continue to increase in the future, irreparable damage to discrete organs (ie. liver) could occur and reproductive capabilities may be reduced. Recruitment of plerocercoids by walleye is likely to continue because their preferred prey, the yellow perch, are so heavily infected. Even if walleye switched to another prey resource, the number of infected forage species in Lake of the Woods means transmission of plerocercoids would still occur. Eradication of the definitive host could be the only solution to ensure that walleye do not continue to obtain plerocercoids in the future. Even maintaining control on present population levels of the parasite in Lake of the Woods would be very difficult mainly because of the size of the system and because smallmouth bass appear to be firmly established.

LITERATURE CITED

Arme, C. and R. W. Owen. 1968. Occurrence and pathology of *Ligula intestinalis* infections in British fishes. J. Parasitol. 54: 272-280.

Bagenal, T. B. and E. Braum. 1978. Eggs and early life history. *In* Methods of Assessment of Fish Production in Fresh Waters. *Edited by* T. B. Bagenal. Blackwell Scientific Publications, Oxford.

Bailey, W. C. 1984. Epizootiology of *Posthodiplostomum minimum* (MacCallum) and *Proteocephalus ambloplitis* (Leidy) in bluegill (*Lepomis macrochirus* Rafinesque). Can. J. Zool. 62: 1363-1366.

Bangham, R. V. 1925. A study of the cestode parasites of the black bass in Ohio with special reference to the life history and distribution. Ohio J. Sci. 25: 255-270.

Bangham, R. V. 1927a. Life history of bass cestode *Proteocephalus ambloplitis* . Trans. Am. Fish. Soc. 57: 206-209.

Bangham, R. V. 1927b. Parasites as a limiting factor in Ohio fish hatcheries. J. Parastiol. 13: 214.

Bangham, R. V. 1941a. Parasites from fish of Buckeye Lake, Ohio. Ohio J. Sci. 41: 441-448.

Bangham, R. V. 1941b. Parasites of fish from Algonquin Park Lakes. Trans. Am. Fish. Soc. 70: 161-171.

Bangham, R. V. 1955. Studies on the fish parasites of Lake Huron and Manitoulin Island. Am. Midl. Nat. 53: 184-194.

Bangham, R. V. and G. W. Hunter III. 1939. Studies of fish parasites of Lake Erie. Distribution studies. Zoologica (N. Y.). 24: 385-448.

Bauer, O. N. 1984. Soviet investigations on the population biology of fish parasites. J. Fish Biol. 25: 545-550.

Becker, C. D. and W. D. Brunson. 1968. The bass tapeworm: A problem in northwest trout management. Prog. Fish-Cult. 30: 76-83.

Befus, A. D. and R. S. Freeman. 1973. Life cycles of two Corallobothriin cestods (Proteocephaloidea) from Algonquin Park, Ontario. Can. J. Zool. 51: 249-257.

Bulkley, R. V., V. L. Spykermann and L. E. Inmon. 1976. Food of the pelagic young-of-year walleyes and five cohabiting fish species in Clear Lake, Iowa. Trans. Am. Fish. Soc. 105: 77-83.

Carlander, K. D. 1945. Age, growth, sexual maturity and population fluctuations of the yellow pike-perch, Stizostedion vitreum vitreum (Mitchill), with reference to the commercial fisheries of Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. 73(1943): 90-107.

Carlander, K. D. 1949. Some trends in the commercial fisheries of Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. 77: 13-25.

Clady, D. M. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in northern Michigan. Am. Mid-Naturalist. 91: 453-459.

Colby, P. J., R. E. McNicol and R. A. Ryder. 1979. Synopsis of the biological data on the walleye, Stizostedion vitreum vitruem (Mitchill 1818). F. A. O. Fish. Synops., No. 119. Rome.

Cooper, A. R. 1915. Contributions to the life history of Proteocephalus ambloplitis Leidy, a parasite of black bass. Contrib. Can. Biol. Fish. Ottawa, 1911-1914. Fasc. 2.

Daniel, W. W. 1978. Applied Nonparametric Statistics. Houghton Mifflin Company, Boston.

Dechtiar, A. O. 1972. Parasites of fish from Lake of the Woods, Ontario. J. Fish. Res. Board Can. 29: 275-283.

Ellis, A. E. 1977. The leucocytes of fish: A review. J. Fish Biol. 11: 453-491.

Elrod, J. H., W. D. N. Busch, B. L. Griswald, C. P. Schneider and D. R. Wolfert. 1981. Food of white perch, rock bass and yellow perch in eastern Lake Ontario. N. Y. Fish and Game J. 28: 191-201.

Esch, G. W. and W. J. Huffines. 1973. Histopathology associated with endoparasitic helminths in bass. J. Parasitol. 59: 306-313.

Esch, G. W., W. C. Johnson and J. R. Coggins. 1975. Studies on the population biology of Proteocephalus ambloplitis (Cestoda) in the smallmouth bass. Proc. Okla. Acad. Sci. 55: 122-127.

Eure, H. 1976. Seasonal abundance of _P. amboplitis_ (Cestoidea: Proteocephalidea) from largemouth bass living in a heated reservoir. Parasitol. 73: 205-212.

Evermann, B. W. amd H. Latimer. 1910. The fishes of the Lake of the Woods and connecting waters. Proc. U.S. National Museum. 39: 121-136.

Finn, J. P. and N. O. Nielson. 1971. The inflammatory response of rainbow trout. J. Fish Biol. 3: 463-478.

Fischer, H. 1972. Studies on the life cycles and ecology of _Proteocephalus ambloplitis_ , _P. fluviatilis_ and _P. pearsei_ (Cestoda) from Lake Opeongo, Algonquin Park. Ph.D. Thesis. University of Toronto, Toronto.

Fischer, H. and R. S. Freeman. 1969. Penetration of parenteral plerocercoids of _Proteocephalus ambloplitis_ (Leidy) into the gut of smallmouth bass. J. Parasitol. 55: 766-774.

Fischer, H. and R. S. Freeman. 1973. The role of plerocercoids in the biology of _Proteocephalus ambloplitis_ (Cestoda) maturing in smallmouth bass. Can. J. Zool. 51: 133-141.

Fischthal, J. H. 1947. Parasites of northern Wisconsin fishes. 1. The 1944 survey. Trans. Wisc. Acad. Sci. Arts and Letters. 37: 157-220.

Fischthal, J. H. 1950. Parasites of northern Wisconsin fishes. II. The 1945 survey. Trans. Wisc. Acad. Sci. Arts and Letters. 40: 87-113.

Fraser, P. G. 1960. The occurrence of _Diphyllobothrium_ in trout with special reference to an outbreak in the west of England. J. Helminthol. 34: 59-72.

Freeman, R. S. 1964. On the biology of _Proteocephalus parallacticus_ MacLulich (Cestoda) in Algonquin Park, Canada. Can. J. Zool. 42: 387-408.

Freze, V. I. 1965. Essential of Cestodology. Vol. V. Proteocephalata in fish, amphibians and reptiles. I. P. S. T. Press. Jerusalem.

Harley, J. P. 1977. Parasites of the white crappie from Lake Wilgreen, Kentuckey. Trans. Ky. Acad. Sci. 38: 136-138.

Harley, J. P. and T. L. Keefe. 1970. Helminth parasites of four species of sunfishes (Centrarchidae) from Lake Wilgreen in Kentuckey. Trans. Ky. Acad. Sci. 32: 71-74.

Henricson, J. 1978. The dynamics of infection of Diphyllobotrium dendriticum (Nitzsch) and D. ditremum (Creplin) in the char Salvelinus alpinus (L.) in Sweden. J. Fish Biol. 13: 51-71.

Hoffman, G. L. 1967. Parasites of North American freshwater fishes. University of California Press, Berkeley.

Hoffman, G. L. 1975. Lesions due to internal helminths of freshwater fish. In Pathology of Fishes. Edited by W. E. Ribelin and G. Migaki. The University of Wisconsin Press, Madison, Wisconsin. pp. 151-187.

Hoffman, G. L. and C. E. Dunbar. 1961. Mortality of eastern brook trout caused by plerocercoids (Cestoda: Pseudophyllidea: Diphyllobothriidae) in heart and viscera. J. Parasitol. 47: 399-400.

Holloway, J. A. 1984. An ecological study of the cestode Schistocephalus solidus in the three-spined stickleback, Gasterosteus aculeatus , at Matamek Lake, Quebec. MSc. Thesis. Institutue of Parasitology, McGill University, Montreal.

Hoole, D. and C. Arme. 1983. Ligula intestinalis (Cestoda: Pseudophyllidea): an ultrastructural study on the cellular response of roach fry, Rutilus rutilus . Int. J.. Parasitol. 13: 359-363.

Hubert, W. A. and M. B. Sandheinrich. 1983. Patterns of variation in gill-net catch and diet of yellow perch in a stratified Iowa lake. N. Am. J. Fish. Manage. 3: 156-162.

Humason, G. L. 1979. Animal Tissue Techniques. 4th ed. W. H. Freeman and Company, San Francisco.

Hunter, G. W. III. 1928. Contributions to the life cycle of Proteocephalus ambloplitis (Leidy). J. Parasitol. 14: 229-242.

Hunter, G. W. III and A. V. Hunninen. 1934. Studies on the plerocercoid larvae of the bass tapeworm Proteocephalus ambloplitis (Leidy) in the smallmouth bass. Suppl. 23rd. Ann. Rep. New York State Conserv. Dept. 1933. pp. 255-261.

Hunter, G. W. III and W. S. Hunter. 1929. Further studies on the bass tapeworm, Proteocephalus ambloplitis (Leidy). Suppl. to the 18th Ann. Rept. N. Y. State Conserv. Dept. Biological Survey, pp. 198-207.

Hunter, G. W. III and J. S. Rankin. 1940. Parasites of northern pike and pickerel. Trans. Am. Fish. Soc. 69: 268-272.

Kelso, J. R. M. and F. J. Ward. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. J. Fish. Res. Board Can. 34: 1655-1669.

Langlois, T. N. 1936. Bass tapeworm infection in a rearing pond. Trans. Am. Fish. Soc. 66: 364-366.

Leidy, J. 1887. Notice on some parasitic worms. Proc. Acad. Nat. Sci. Philad. 39: 20-24.

Lillie, R. D. 1954. Histopathologic technic and practical histochemistry. The Blakiston Co., Inc, New York.

MacLulich, D. A. 1943. Parasites of trout in Algonquin Provincial Park, Ontario. Canadian J. Res. Sect. D. Vol. 21. No. 12. pp. 405-412.

McCormick, J. H. and G. N. Stokes. 1982. Intraovarian invasion of smallmouth bass oocytes by Proteocephalus ambloplitis (Cestoda). J. Parasitol. 68: 973-975.

McDaniel, J. S. and H. H. Bailey. 1974. Seasonal population dynamics of some helminth parasites of centrarchid fishes. The Southwestern Nat. 18: 403-416.

Merritt, R. W. and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Co. Dubuque, Iowa.

Meyer, M. C. and O. W. Olsen. 1971. Essentials of parasitology. Wm. C. Brown Company Publishers, Dubuque, Iowa.

Mithchill, L. G., J. Ginal and W. C. Bailey. 1983. Melanotic visceral fibrosis associated with larval infections of Posthodiplostomum minimum and Proteocephalus spp. in bluegill, Lepomis macrochirus Rafinesque, in central Iowa, U.S.A. J. Fish Diseases. 6: 135-144.

Moore, E. 1925. The inhibition of the spawning function of the smallmouth bass by a parasitic flat-worm. Trans. Am. Fish. Soc. 55: 33-36.

Morrison, G. R. 1957. The incidence and distribution of the bass tapeworm (Proteocephalus ambloplitis) in southern New Hampshire waters. New Hampshire Fish and Game Dept. Manage. Res. Div. Tech. Circ. No. 13.

Nelson, W. R. 1968. Embryo and larval characteristics of sauger, walleye and their reciprocal hybrids. Trans. Am. Fish. Soc. 97: 167-174.

Nie, H. N., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical Package for the Social Sciences. 2nd ed. McGraw-Hill Book Company, New York.

Pearse, A. S. 1924. The parasites of lake fishes. Trans. Wisc. Acad. Sci. Arts and Letters. 21: 161-194.

Pennak, R. W. 1978. Freshwater Invertebrates of the United States. 2nd ed. Wiley-Interscience Publications. John Wiley & Sons, Toronto.

Pennycuick, L. 1971. Quantitative effects of three species of parasites on a population of three-spined sticklebacks, Gasterosteus aculeatus . J. Zool. Lond. 165: 143-162.

Priegel, G. R. 1969a. Age and growth of the walleye in Lake Winnebago. Trans. Wisc. Acad. Sci. Arts and Letters. 57: 121-133.

Priegel, G. R. 1969b. Food and growth of young walleyes in Lake Winnebago, Wisconsin. Trans. Am. Fish. Soc. 98: 121-124.

Roberts, R. J. 1978. Fish Pathology. Bailliere Tindall, London.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, W. B. Scott. 1980. A list of common and scientific names of fish from the United States and Canada. 4th ed. Am. Fish. Soc. Special Pub. No. 12.

Rosen, R. and T. A. Dick. 1984. Growth and migration of plerocercoids of Triaenophorous crassus Forel and pathology in experimentally infected whitefish, Coregonus clupeaformis (Mitchill). Can. J. Zool. 62: 203-211.

Scott. W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184.

Serns, S. L. 1982. Walleye fecundity, potential egg deposition and survival from egg to fall young-of-year in Escanaba Lake, Wisconsin, 1979-1981. N. Am. J. Fish. Manage. 4: 388-394.

Siefert, R. E. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner and rainbow smelt. Trans. Am. Fish. Soc. 101: 219-225.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman and Company, San Francisco.

Sommerville, C. 1981. A comparative study of the tissue response to invasion and encystment by Stephanochasmus baccatus (Nicoll, 1907) (Digenea: Acanthocolpidae) in four species of flatfish. J. Fish Diseases. 4: 53-58.

Sutherland, D. R. and H. L. Holloway Jr. 1979. Parasites of fish from the Missouri, James, Sheyenne, and Wild Rice Rivers in North Dakota. Proc. Helminthol. Soc. Wash. 46: 128-134

Sweeting, R. A. 1976. Studies on Ligula intestinalis (L.) effects on a roach population in a gravel pit. J. Fish Biol. 9: 515-522.

Swenson, W. A. and L. L. Smith Jr. 1976. Influence of food competition, predation and cannibalism on walleye (Stizostedion vitruem vitreum) and sauger (S. canadense) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. 33: 1946-1954.

Tedla, S. and G. H. Fernando. 1970. On the characterization of the parasite fauna of yellow perch (Perca fluviatilis) in five lakes, in southern Ontario, Canada. Helminthologia. 11: 23-33.

VanCleave, H. J. and J. F. Mueller. 1934. Parasites of the Oneida Lake fishes. Roosevelt Wildl. Annals. 3: 280-287.

Weber, J. J. and B. L. Les. 1982. Spawning and early life history of yellow perch in the Lake Winnebago system. Wisc. Dept. Nat. Res. Tech. Bull. No. 130.

Wolfert, D. R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. J. Fish. Res. Board Can. 26: 1877-1888.